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MUSCULAR pH AND RELATED TRAITS IN RABBITS : A REVIEW

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ABSTRACT : After reviewing muscular biology and general relationships between muscular physico-chemistry and meat quality, this review analyses the variations in muscular pH and related traits in rabbits. Among biological factors (muscle, age, genotype, family), ***muscle*** factor is the most important. It determines the differences in ultimate pH (pHu) between muscles, which can reach 0.7 units and which are due to differences in the fibre typology. Increase in glycolytic metabolism during muscle ***growth*** is accompanied by pHu lowering; its variation depends on the precocity of muscle development. Comparative studies of ***breeds*** do not show any evidence of differences in pH above 0.2 units; no breed presents abnormal acidification or pHu kinetics, which might entail anomalies in Water Holding Capacity or other qualitative traits in meat. ***Within breed***, the existence of correlations between pHu and growth characteristics may lead to a reduction in meat quality when strains are selected for weight productivity. The effect of ***dietary factors*** is relatively small. When they can be detected, pH variations mostly correspond to modifications in growth rate. Thus the pHu of meat is lowered when growth is stimulated by a high level of nutrition or a high protein content. ***Slaughter factors*** have a marked influence on muscular pH. Transport leads to a noticeable rise in pHu, a result of *ante mortem* depletion of glycogenic reserves; when subjected to prolonged stress, meat is darker and has a higher water holding capacity. Electroanaesthesia accelerates muscular acidification without modifying pHu. ***Carcass chilling*** slows down the physico-chemical processes of *rigor mortis*: it slows down the fall in pH and reduces the intensity of sarcomere retraction. Even when chilling is intense, in spite of some contradictions in published literature, the phenomenon of *"cold shortening"* does not seem to be of major significance in rabbits. During ***meat storage*** in refrigerated form, after a certain latency period, the maturation processes are witnessed by de-amination of the proteins and thus by a raised pH. Freezing slows down this process, but does not avoid a rise in pH after several months in storage.

RESUME : Variations du pH musculaire et caractères corrélés chez le lapin. Une revue.
Après des rappels sur la biologie musculaire et sur les relations générales existant entre la physico-chimie musculaire et la qualité de la viande, la présente revue analyse les variations du pH musculaire et les caractères corrélés chez le lapin. Parmi les facteurs biologiques (muscle, âge, type génétique, famille), le facteur ***muscle*** est le plus important. Il détermine des écarts de pH ultime (pHu) entre muscles pouvant atteindre 0,7 unité, qui sont dus à des différences de typologie des fibres constitutives. L'augmentation du métabolisme glycolytique au cours de la ***croissance*** musculaire s'accompagne d'une diminution du pHu, son évolution dépendant de la précocité de développement des muscles. Les études comparatives de ***races*** ne mettent pas en évidence d'écarts de pH supérieurs à 0,2 unités ; aucune race ne présente de cinétique d'acidification ou de pHu anormaux, susceptibles d'entraîner des anomalies du Pouvoir de Rétention d'Eau et des autres caractères qualitatifs de la viande. ***Intra-souche***, l'existence de corrélations génétiques négatives entre le pHu et les caractères de croissance peut conduire à une dégradation de la qualité de la viande sous l'effet de la sélection des souches sur la productivité pondérale. L'influence des ***facteurs alimentaires***, est relativement discrète. Lorsqu'elles sont observées, les variations de pH sont, le plus souvent, corrélatives de modification de la croissance. Ainsi le pHu de la viande est abaissé lorsque la croissance est stimulée par un niveau alimentaire ou par un niveau protéique élevés. Les ***facteurs d'abattage*** ont une incidence marquée sur le pH musculaire). Le transport conduit à une élévation sensible du pHu, par suite de la déplétion *ante mortem* des réserves glycogéniques, sous l'effet du stress prolongé ; la viande plus sombre, a alors un pouvoir de rétention d'eau accru. L'électroanesthésie accélère l'acidification musculaire sans modifier le pHu. La ***réfrigération des carcasses*** freine les processus physico-chimiques de la *rigor mortis* : elle ralentit la chute du pH et réduit l'intensité de la contraction des sarcomères. Même lorsque la réfrigération est intense, malgré quelques contradictions trouvées dans la littérature, le phénomène de contracture au froid, "cold shortening", n'apparaît pas préoccupant chez le lapin. Pendant le ***stockage*** de la viande à l'état réfrigéré, après une certaine latence, les processus de maturation se manifestent par une désamination des protéines et donc par une élévation du pH. La congélation freine ce processus mais n'évite pas une augmentation du pH après plusieurs mois de stockage.

[Le texte français de cette revue est disponible auprès des auteurs]

INTRODUCTION

Muscular tissue is highly differentiated and specialised. It is within the muscle that the transformation of chemical energy into mechanical energy occurs. Meat is the result of *post mortem* changes characterized by two groups of biochemical events: the onset of *rigor mortis* and the maturation process. The first phase and its principal expression, muscular acidification, have been studied extensively. Muscular pH is an interesting trait for two reasons. Firstly, it acts as a general estimator of fibre typology, of the balance of the energy metabolism pathways and of the level of energy reserves in the muscles, the latter being also dependent on *ante mortem* treatment. Secondly, it allows certain qualitative characteristics of the meat to be predicted. After a brief review of muscular physiology and the general relationships that exist between the acidity of meat and its technological and sensory qualities, this study will go on to examine the biological, zootechnical and technological factors which influence muscular pH and related traits.

1. GENERAL ACCOUNT

1.1. MUSCULAR TISSUE

The chemical composition of muscle varies, according to animals, species and type of muscle, from 75 to 80% water, 15 to 22% protein, 1 to 15% lipids, 1

to 2% carbohydrates, 1% non-protein nitrogen and the same amount of mineral salts (LAWRIE, 1968a). From an anatomical point of view, skeletal muscles are composed of muscular fibres, which are the basic contractile units, and also of connective tissue. The latter represents between 0.5 and 5% of the muscular mass. It consists of the *epimysium*, which covers the muscle, the *perimysium*, which delineates the fascicle of muscular fibres and the *endomysium*, which envelops the individual muscle fibres. It also determines the basic toughness in the meat of old animals. Its main constituents are collagen (around 70 to 80% of dry matter) and elastin. The muscular fibres represent between 75 and 90% of total muscle volume. The specificity of the syncitial cells lies in the contractile ability of their myofibrillary proteins, which represent more than 50% of total proteins (Figure 1).

The phenomena of muscular contraction and relaxation correspond to the cycles of attachment, slippage and detachment of the actin and myosin molecules, with troponin and tropomyosin intervening as regulating proteins (EBASHI and ENDO, 1968). This contraction and relaxation of fibres is made possible due to energy created by the hydrolysis of ATP (adenosine triphosphate) in the presence of calcium (1):

$$\text{(1)}\ ATP + H_2O \xrightarrow{\text{myosin ATPase, } Ca^{++}} ADP + P_i + H^+ + \text{energy}$$

The metabolism of energy in muscle tissue can be characterised by the major role played by sugars. Depending on whether the muscle fibres have a preponderantly oxidative pathway for catabolising glucose or an anaerobic one (formation of lactates), it can be distinguished "red" fibres (rich in mitochondria and myoglobin) and "white" fibres (low in mitochondria and rich in glycogen). These fibres have a rapid or slow

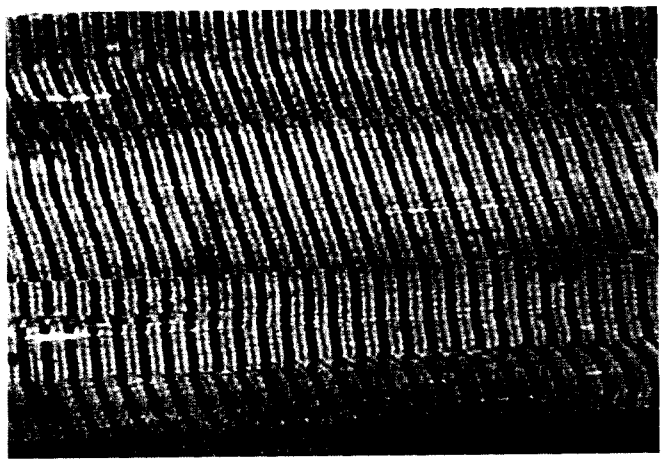

Figure 1 : Transversal striation of myofibres resulting from myofibrillar protein structure (photo OUHAYOUN)

Table 1 : Main properties of the different types of fibres (after BACOU and VIGNERON, 1988).

	αW	αR	βR
Diameter	+++	+	+
Vascularisation	+	++	+++
Contraction speed	+++	+++	+
Glycolitic metabolism	+++	++	+
Oxidative metabolism	+	++	+++
Myoglobin content	+	+++	+++
Glycogen content	+++	+++	+
Lipid content	+	++	+++

contraction rate respectively, depending on the structure of the constituent myosin molecules, which determines a strong or weak ATPasic activity. One of the most commonly used nomenclatures for the classification of muscle fibres is that of ASHMORE and DOERR (1971) which distinguish:

- αW *rapid twitch white* fibres, characterised by a dominant glycolytic metabolism and a high ATPasic activity,
- αR *rapid twitch red* fibres, with an oxydo-glycolytic metabolism and a high ATPasic activity,
- βR *slow twitch red* fibres, with an oxidative metabolism and a low ATPasic activity.

Most muscles are heterogeneous mixtures of these three fibre types (Table 1). Muscles are called "*white*" or "*glycolytic*" if they contain a high proportion of αW fibres,"*red*" or "*oxidative*" if they are composed of a majority of βR and αR fibres, or *mixed*. However, the typology of the fibres differ with age and various other factors (Cf. infra).

1.2. EVOLUTION OF MUSCLE INTO MEAT

1.2.1. Biochemical and mechanical phenomena of *rigor mortis*

Slaughter causes a stimulation of the muscular metabolism, after which the muscle no longer depends on its energy reserves to try to maintain its homeostasis. The rapid reduction in partial oxygen pressure means that only anaerobic mechanisms remain functional. Glycogen is the main energy source for the muscle, its rate reaching more than 4.41 µmoles per gram of tissue, after bleeding, in rested animals, versus only a few µmoles of phosphocreatin.

The onset of *rigor mortis* occurs as a result of the depletion of energy reserves in the muscle (ATP, creatin phosphate, glycogen) and the reduction of its elastic properties. The ATP is hydrolysed following equation

(1) above. It is regenerated *via* exclusively anaerobic pathways.

Degradation of the phosphocreatin, which is linked to a phosphorylation of the ADP, is catalysed by *creatin phosphokinase*, allows ATP to be effectively resynthesized and its concentration to be maintained; but the phosphocreatin is quickly exhausted. Another minor reaction, which is catalysed by *myokinase*, allows the synthesis of ATP (and of AMP) from 2 ADP.

The phosphorolysis of glycogen, which is catalysed by *phosphorylase* - first activated in the "adenylcyclase" system involving AMP and catecholamins - leads to the production of glucose 1P. Each molecule of glucose 1P is first transformed into glucose 6P (*phospho-glucomutase*) and is then broken down within the glycolysis cycle to produce three molecules of ATP and two lactates (2):

(2) 3 ADP + 3 P_i + H^+ + glucose (n) ----> 3 ATP + 2 lactates + glucose (n-1)

The result of one (2) reaction and of three (1) reactions is the release of two protons per molecule of glucose transformed, i.e. one proton per molecule of lactate produced:

glucose (n) + 3 H_2O ----------> glucose (n-1) + 2 lactates + 2 H^+

Whereas muscular pH is nearly neutral in the living animal, it progressively achieves a relatively stable value, its ultimate pH, which lies between 5.3 and 6 (Figure 2). The pH of meat, which is a semi-solid, is that of its liquid phase; it is defined as the cologarithm of its concentration in proteins: pH = - log [H^+].

Glycolysis ceases either through a lack of degradable glycogene or by deamination of the AMP, an intervening co-factor in the activation of the *phophorylase*. In the latter case, glycogen can persist in the muscle, even when ultimate pH is achieved. ATP levels decrease rapidly, as glycolysis is a relatively inefficient mechanism of synthesis. In fact, for each

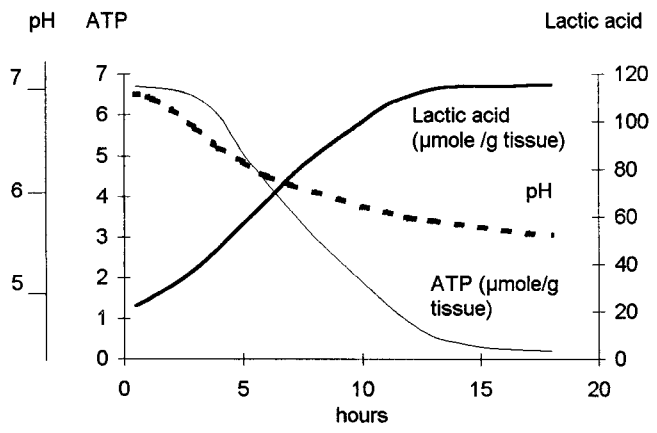

Figure 2 : *Post mortem* evolution of biochemical components and pH in rabbit muscle at 19°C (after ITO *et al.*, 1986)

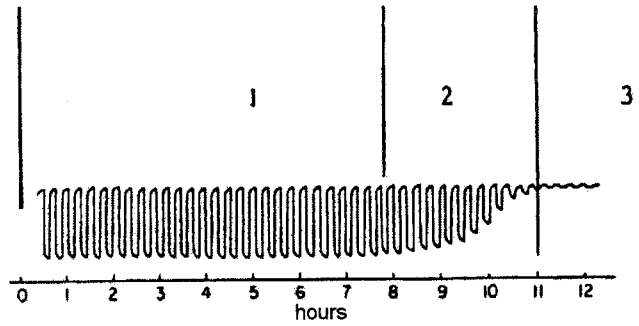

Figure 3 : Evolution of extensibility of the *Psoas major* muscle during the onset of *rigor mortis*, correlated with pH fall (from 7.0 to 5.7) (17°C) (after BENDALL, 1973)

molecule of glucose degraded, it only supplies 3 molecules of ATP, versus 37 in the course of respiration. When ATP levels have reduced by approximately one half, actin and myosin molecules combine to form actomysin; the entire myofibrillary apparatus becomes rigid.

BENDALL (1973a) describes three phases in the establishment of *rigor mortis* in rabbits (Figure 3):

1) a *latency phase*, during which the muscle extensibility remains the same as at the time of slaughter; it should be noted that the duration of this phase can be practically zero in exhausted animals, the lack of reserves hindering ATP synthesis;
2) a proper *onset phase*, which sees a rapid decrease of extensibility;
3) a *phase* of inextensibility.

The *post mortem* variation in pH can be characterised by its rate of fall, which is in proportion to the ATPasic activity of the myosin, and by its amplitude, which depends on the quantity of glycogen degraded (or of lactate produced).

The initial level of reserves is determined by biological factors (muscle, age, sex, genetic type) and also husbandry factors (herd management, feeding). These factors also influence the typology of the muscular fibres and therefore the proportions of isozymes of the myosin - and in turn ATPasic activity -, the level of glucidic reserves and the buffering power of the tissue. The level of reserves and their evolution can also be determined by technological factors (*ante mortem* treatments of the animals, carcass storage temperature). For example, the continuous stress caused by transportation to the slaughterhouse reduces muscular carbohydrate levels in favour of hepatic levels and consequently limits the muscle acidification and accelerates the onset of *rigor mortis*. Resting the animals before slaughter restores, to a certain extent, acidification potential.

The biochemical processes of *rigor mortis* can be accelerated by a rise in temperature, whether this is

induced experimentally or by stress preceding slaughter. In the case of stress, the discharge of catecholamines accelerates the processes of glycolysis, hydrolysis of the ATP and muscular acidification; onset of *rigor mortis* is accelerated and the latter therefore increases in intensity.

Rapid chilling can also cause an abnormal *rigor mortis*, but only if it is applied when muscular pH is above 6 and the environment is rich in ATP. This "cold shortening" (LOCKER and HAGYARD, 1963) results from the activation of ATPases by Ca^{++} ions, which are released at low temperatures by the sarcoplasmic *reticulum*. This "cold shortening" develops not only in rapidly cooled muscular tissue, but also ("thaw *rigor*") when muscles frozen before the onset of *rigor mortis* are defrosted.

1.2.2. Maturation

According to a classic point of view the maturation takes place after the onset of *rigor mortis*. In reality, most of the hydrolytic phenomena which characterise maturation begin in the first moments after slaughter.

Glycogen can be converted through glycolysis and too through Sharp way. In this latter, it is splitted into glucose under the combined action of amylase, amylo 1-6 glucosidase and maltase (SHARP, 1957). AMP, whose role in the activation of phosphorylase has been described above, is deaminated then dephosphorylated into hypoxanthine. This compound is both a maturation indicator and a flavour enhancer. However, the main feature of maturation is to be found in the process of hydrolysis of the contractile apparatus under the influence of proteases (CAF and cathepsins), each of which is active at a specific pH. The proteolyse progressively reduces myofibrillary toughness. Muscular pH, having reached a final level determined by *ante mortem* energy reserves, thereafter tends to increase under the influence of deamination reactions (AMP, free amino-acids). These new biochemical events have a wide-ranging influence on the technological and sensory qualities of the meat.

1.3. RELATIONSHIPS BETWEEN MUSCULAR PH AND MEAT QUALITY

pH has an important influence on the keeping qualities of meat. As well as affecting protein structures and water holding capacity, it also affects the sensory qualities of meat, in particular colour and tenderness.

1.3.1. Water holding capacity (WHC)

WHC measures the capacity of the meat to retain, in strictly defined conditions, its own water content or water that has been added. It affects the appearance of raw meat and the tenderness of cooked meat by means of losses during cooking. HAMM (1960) assumed that water in the muscle is present in two forms: one which is strongly linked to proteins and the other in free form immobilised in the tissue. Variations in WHC only affect water in free form. But the scale of this fraction is poorly defined as it depends on the method used to extract the water (natural draining, pressure, centrifugal force, cooking).

Post mortem acidification reduces WHC. In fact, when pH nears the isoelectric point of the myofibrillary proteins, which is around 5.0, the net charge of the latter lowers, the myofibrillary network schrinks and the capacity available for water decreases. This schrinkage of the network is amplified by the fixation of bivalent ions (Ca^{++} et Mg^{++}) into the negative charges of the proteins. Finally, the denaturation of sarcoplasmic and myofibrillary proteins, which can be a result of a rapid pH fall at a high temperature, intensifies the reduction in WHC. This reaches its minimal value at the end of *rigor mortis* onset, when myofibrillary volume is reduced by approximately 40%, both as a result of the formation of actomycin complex and of structural modifications of proteins by acidification (OFFER, 1984)..

Meat from animals exhausted before slaughter, whose ultimate pH is high, presents a high WHC and, correlatively, a firm and dry consistency. The ability of this meat to absorb water during pickling in brine treatment or soaking is then increased.

1.3.2. Tenderness

Tenderness is one element in the range of mechanical sensations encountered during mastication. It is a measure of the ease with which meat can be divided up and dispersed. It forms a basic criterion for most consumers. In fact, a minimum level of tenderness is required before they will appreciate other qualities such as juiciness - which also depends on the WHC - and flavour. Tenderness depends on the quantity and quality of the connective tissue and especially, in the meat of young animals, on the structure of the myofibrillary system, which is determined by the conditions of *rigor mortis* onset and its resolution (maturation). Tenderness is also connected to pH, by means of its direct influence on WHC. Thus" PSE" (pale, soft, exsudative) meats for example, are particularly tough.

1.3.3. Colour

The colour of meat depends on the level of myoglobin, its state of oxydo-reduction, the degree of oxidation of the iron atom in the heme and on a possible denaturation of the globin. The brightness of meat rises as the muscle acidifies. This causes the myofibrillary apparatus to schrink and thus the reflection of light from the surface to increase. In" PSE" meats, denaturation of the myoglobin and oxidation of the pigment in

metmyoglobin intensifies the brightness due to pH acidity. Any factor, such as stress or exhaustion, that causes an *ante mortem* depletion of glycogenic reserves will raise ultimate pH and at the same time reduce the meat brightness. In extreme cases, complete exhaustion of the reserves leads to meats known as "DFD" (dark, firm, dry), which are characterised by a dark red section and a very high pH. Resting before slaughter has an inverse effect in so far as it tends to restore muscular acidification potential. When the brightness of the meat is measured on the aponeurosis rather than on a fresh muscular section, the structure of the former, in particular its hydration state, can mask its correlative effects with pH.

1.3.4. Storage ability

pH values determine environmental microbial balance. Low pH has a bacteriostatic effect. On the other hand, meat with a pH above 6 is generally considered unsuitable for conservation. In fact, the low level of carbohydrates in meat favours proteolytic micro-organisms.

2. MUSCULAR pH AND RELATED TRAITS IN RABBIT

The pH in meat can be measured either *in situ*, by inserting an electrode, or *in vitro*. The latter is performed on muscular tissue crushed in a solution of sodium iodo-acetate which blocks glycolysis and stabilises pH. Being precise and repeatable, this measure is particularly well adapted to muscles with a high pH and muscles in the early stages of acidification, in which the availability of the liquid phase is minimal. For ultimate pH, there is a strong correlation between the two techniques: r = 0.92 and r = 0.85 for the *Longissimus dorsi* and *Biceps femoris* muscles respectively (OUHAYOUN and DELMAS, 1988) (Figure 4).

In live rabbits, muscular pH is approximately neutral (BATE-SMITH and BENDALL, 1949). It decreases rapidly immediately after slaughter, then more slowly afterwards. In the *Biceps femoris* muscle of crossbred rabbits of both sexes at 77 days of age, pH value decreases from 6.4 (± 0.24) to 5.8 (± 0.09) between 30 minutes and 24 hours, when the carcasses are chilled at 4°C, and after one hour of preparation in an slaughter house at 10°C (OUHAYOUN *et al.*, 1973). Within this time-scale, the pH of the *Biceps femoris* reduces exponentially following the equation $pH = 6.39^{e\text{-}079.10\text{-}4\ t}$ (OUHAYOUN and DELMAS, 1988). Twenty hours after slaughter, pH can be considered to have reached its ultimate value.

Buffer power, which is determined by non-protein nitrogen levels in the muscular tissue, affects acidification. According to HADDAD *et al.* (1994b), buffer power is at its maximum between pH 7.23 and 6.28 and at its minimum between pH 5.45 and 4.99. Muscular acidification is therefore slower, especially during the first hour *post mortem*.

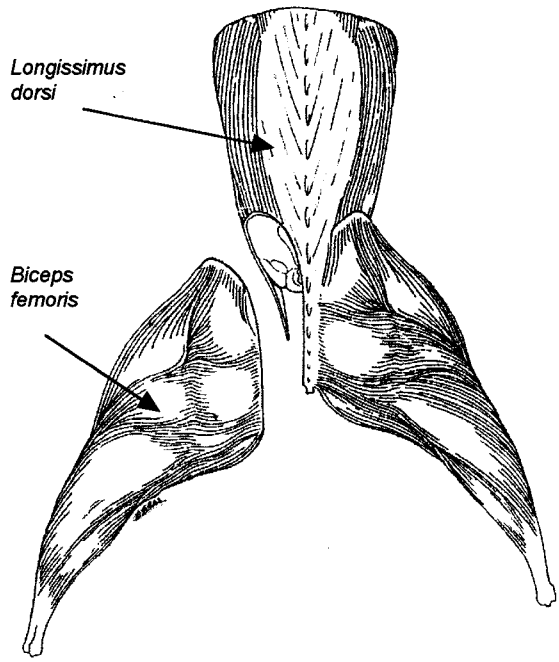

Figure 4 : Anatomical location of *Longissimus dorsi* and *Biceps femoris* muscles, the most often studied in meat technology research (after BLASCO and OUHAYOUN, 1996 ; picture Y. GRAS)

2.1. INFLUENCE OF BIOLOGICAL FACTORS

2.1.1. Variation between muscles

Many studies report differences between muscles in the acidification process and in ultimate pH (pHu) (NIEDZWIADEK *et al.*, 1983; NATH and RAO, 1985; RENOU *et al.*, 1986; RISTIC, 1986; OUHAYOUN and DELMAS, 1988; DELMAS and OUHAYOUN, 1990; OUHAYOUN *et al.*, 1990a; BLASCO and PILES, 1990; XICCATO *et al.*, 1990; OSMAN, 1991; PARIGI-BINI *et al.*, 1992; LAMBERTINI *et al.*, 1996).

Studies dealing with "initial" pH (pHi) are difficult to interpret, as the time of measurement is often imprecisely defined, given the high rate of muscular acidification in the first hour following slaughter.

The sooner after slaughter the pH measurements, the greater the differences between muscles pH.. For example, according to OUHAYOUN *et al.* (1990a), in a sample of 11 muscle sites, pH measured 3 hours after slaughter lies between 6.08 and 6.78, whereas ultimate pH (22h) lies between 5.71 and 6.00.

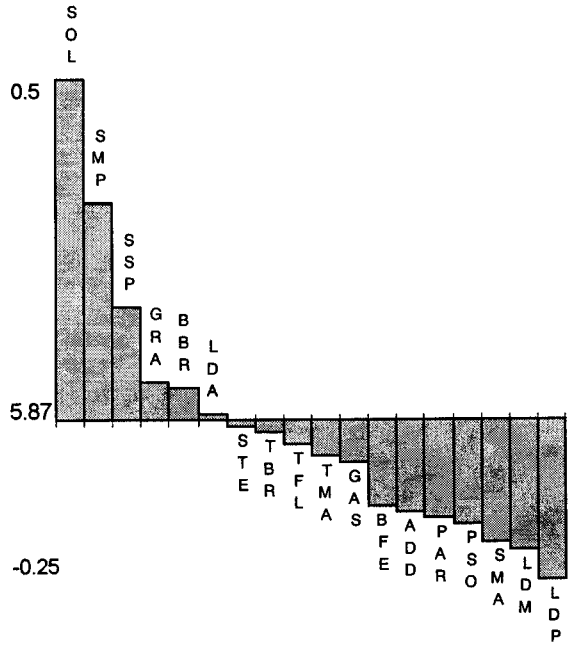

Figure 5a : Ultimate pH of 18 muscular locations. Overall mean and deviations (after OUHAYOUN and DELMAS, 1988)

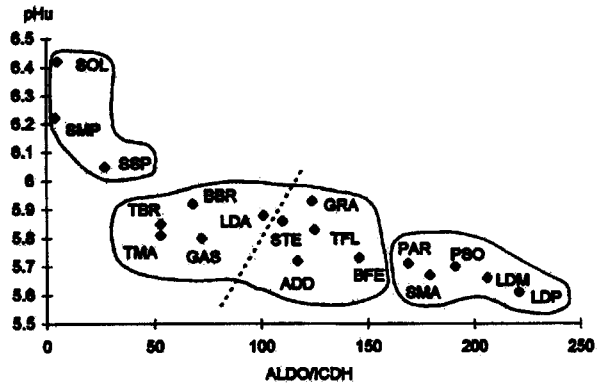

Figure 5b : Relationship beetween ultimate pH (pHu) and energy metabolism (aldolase/ICDH ratio) (after DELMAS and OUHAYOUN, 1990)

SOL : Soleus; **SMP** : Semimembranosus proprius; **SSP** : Supraspinatus; **GRA** : Gracilis; **BBR** : Biceps brachii; **LDA** : Longissimus dorsi (fore part), **STE** : Semitendinosus; **TBR** : Triceps brachii; **TFL** : Tensor fasciae latae; **TMA** : Teres major; **GAS** : Gastrocnemius; **BFE** : Biceps femoris; **ADD** : Adductor brevis et magnus; **PAR** : Parameralis; **PSO** : Psoas major; **SMA** : Semimembranosus accessorius; **LDM** : Longissimus dorsi (intermediate part); **LDP** : Longissimus dorsi (back part)

The muscles generally differ both by the acidification kinetics and the ultimate pH. For example, the *Biceps femoris* muscle has a lower pH at 15-20 minutes than the *Longissimus dorsi,* but a higher pH at 24 hours (BLASCO and PILES, 1990). The more rapid initial acidification of this "red" muscle can be attributed to two phenomena: 1- a better irrigation which gives it a high slaughter stress susceptibility correlated with a fast glycogenolysis (OUHAYOUN and DELMAS, 1988), 2- a reduced buffer capacity (BENDALL, 1973a; RENOU *et al.*, 1986). The higher ultimate pH of the *Biceps femoris* muscle is depending on its lower glycolytic potential.

However, oftenly, the muscles have the same classification based on the pH measured either at 3 hours or at 22 hours *post mortem*. It means that they differ only by their glycolytic potential (OUHAYOUN *et al.*, 1990a, PARIGI-BINI *et al.*, 1992).

Muscles in the carcass forequarters have a higher ultimate pH than those in the hindquarters. The latter in turn have a higher ultimate pH than those of the loin (NIEDZWIADEK *et al.*, 1983; NATH and RAO, 1985; RISTIC, 1986; DELMAS and OUHAYOUN, 1990; OSMAN, 1991; PARIGI-BINI *et al.*, 1992). This is due to differences in typology of the constituent fibres (OUHAYOUN and VIGNERON, 1975). These typological differences have been quantified using histological (LOBLEY *et al.*, 1977; MCFADDEN *et al.*, 1984; KULISEK and MARENCAK, 1984; KULISKOVA *et al.*, 1985; LAMBERTINI *et al.*, 1996), enzymological (BACOU 1972; BASS *et al.*, 1973; BACOU and VIGNERON 1976a; DELMAS and OUHAYOUN, 1990) and physico-chemical methods (RENOU *et al.*, 1986). Muscles made up of slow red fibres (*Soleus, Semimembranosus proprius)*, rich in oxidative enzymes (*isocitrate dehydrogenase, succinate dehydrogenase*) and low in glycogen, have a high ultimate pH. On the other hand, muscles formed of rapid white fibres (*Psoas major*), rich in glycogen and in glycolytic enzymes (*fructose 1.6 diP aldolase*) have a more acid ultimate pH. The diversity of muscular typology is shown by a continuous pHu spectrum.

Ultimate pH and aldolase / ICDH (fructose 1,6 - diP aldolase / NADP isocitrate-dehydrogenase) levels, which express the relative importance of the two main energy metabolism pathways, allow the classification of muscles into three groups (Figures 5a and 5b);

- Oxidative muscles rich in βR fibres (*Semimembranosus proprius, Soleus, Supraspinatus*),
- Glycolytic muscles, rich in αW fibres (*Parameralis, Semimembranosus accessorius, Psoas major, Longissimus dorsi* - posterior and median parts),
- Intermediary muscles, of which the most oxidative are from the forequarter - the arm (*Triceps brachii, Teres major, Biceps brachii*), or the trunk (*Longissimus dorsi* - anterior part) - and from the leg (*Gastrocnemius*), and the least oxidative those from the thigh (*Semitendinosus, Adductor, Tensor Fasciae Latae, Gracilis, Biceps femoris*).

Between muscles, the pHu has a negative correlation with aldolase activity (r = -0.91) (DELMAS

and OUHAYOUN, 1990) and with the fluid loss of meat during cooking (NIEDZWIADEK *et al.*, 1983). It has a positive correlation with WHC (r = 0.82) and juiciness (r = 0.32) (NATH and RAO, 1985).

These results, which have been obtained by histological, enzymological or physico-chemical methods, add to the coherence of the knowledge on rabbit musculature. The relationships between ultimate pH and energy metabolism allows to map out the muscles for biological and technological experimentations on the species.

2.1.2. Muscular heterogeneity

Ultimate pH varies between different sites in the same muscle (CANTONI *et al.*, 1975). In the *Longissimus dorsi* muscle, the ultimate value decreases from 5.88 to 5.61 running from fore- to hindquarters, with a corresponding increase in the aldolase / ICDH ratio (DELMAS and OUHAYOUN, 1990). This variation is attributable to differences in fibre typology (VIGNERON *et al.*, 1976). In fact, the percentage of βR fibres decreases from around 10% in the forequarter to 3% in the hindquarter, whereas the percentage of αR fibres increases from 34 to 41%. LOBLEY *et al.* (1977) confirm this muscular heterogeneity in *Longissimus dorsi, Semitendinosus, Soleus* and *Semimembranosus proprius.*

This heterogeneity calls for the precise definition of pH measuring sites in technological quality control operations for meat. It probably explains certain discrepancies in the literature.

2.1.3. Growth parameters

A distinction should be drawn between the effect of age and that of weight. In the first case, for each age compared, the natural distribution of individual weights around the general average is preserved. In the second case, the variability of individual weights in each lot is nil.

2.1.3.1. Age

In the course of postnatal metabolic differentiation, muscular energy equilibrium comes to favour more and more the glycolytic pathway, with variations that depend on muscle typology and function (BACOU and VIGNERON, 1976b). The increase in glycolytic energy metabolism, as a function of age, is more pronounced in the *Biceps femoris* muscle than in the *Longissimus dorsi.* This increase is correlated with a decrease in oxidative metabolism, myoglobin level (OUHAYOUN *et al.*, 1983), and in ultimate pH of *Psoas major* (r = -0.57**) and *Longissimus dorsi* muscles (r = 0.71**) (DALLE ZOTTE and OUHAYOUN, 1995). According to the latter authors, the faster the relative growth of muscle, the earlier the development of glycolytic energy metabolism and of ultimate pH level. Thus, the *Soleus* and *Semimembranosus proprius* muscles, which have the same relative development than the carcass, between 28 and 84 days, are not concerned with any change in glycolytic metabolism and ultimate pH after the age of 28 days. On the other hand, the energy metabolism and the ultimate pH of the *Psoas major* and *Longissimus dorsi* muscles, which are less precocious, evolve for longer time (up to 42-56 days and 56-70 days respectively).

Between 9 and 11 weeks of age, average ultimate pH of the five thigh muscles diminishes (5.85 *vs* 5.77) (PERRIER and OUHAYOUN, 1996). The same is true between 10 and 14 weeks for the loin (5.64 *vs* 5.41) and the thigh (5.79 *vs* 5.63) (RISTIC, 1986). The lowering of ultimate pH corresponds to a lowering of WHC in raw meat. OSMAN (1991) observed a tendency to a lowering of pHu between 14 and 18 weeks, as long as pHu is measured at least 24 hours after slaughter, given the relatively slow *post mortem* acidification in old rabbits muscle. This slight lowering of pHu as a function of age has no corresponding effect on WHC in raw meat or on cooking losses, but is associated with a darkening of meat which is due to an accumulation of heminic pigments. Within the same age range (9 to 13 weeks), PARIGI-BINI *et al.* (1992) and BATTAGLINI *et al.* (1994) observed no lowering of pHu during growth in five muscle sites in the thigh and trunk. LAMBERTINI *et al.* (1996), studying rabbits at 75, 85 and 95 days, found the same pHu in the *Biceps femoris* muscle, but a slight increase of the pHu as a function of age in the *Latissimus dorsi* and *Soleus* muscles, when their fibre typology is stable.

2.1.3.2. Intra-age weight

ROIRON *et al.* (1992) observed a tendency towards a lowering of the average pHu of four thigh muscles between the weights of 2.2, 2.4 and 2.6 kg, whether these were attained at 70 or 77 days. For RISTIC (1989) the lowering of pHu as a function of weight (2.6, 2.8 or 3.0 kg) in rabbits from 87 to 93 days is only significant in the loin of one of the two studied breeds. When rabbits are older (112 days), the pHu and the corresponding qualitative traits of the meat are not affected by weight (2.82 *vs* 3.32 kg) (GRASHORN *et al.*, 1996).

Table 2 : Variability of muscle ultimate pH and correlated traits between breeds, strains and crosses.

Authors	Breeds or crossings	Age or weight	Muscle or anatomic part	ultimate pH		WHC (e) %		Cooking loss %		Brightness %	
OUHAYOUN *et al.*, 1974	Terminal crossing with: strain 1 strain 2 strain 8 strain 3 strain 4	77 d	*Biceps femoris*	 5.84 5.83 5.79 5.75 5.83	 *						
OUHAYOUN, 1978	Terminal crossing with: Bouscat Giant Flemish Giant Havane Rex INRA 1027 INRA 1077 INRA 1089 Coloured Dwarf	77 d	*Biceps femoris*	 5.91 5.87 5.91 5.89 5.88 5.87 5.91	 ns						
	Terminal crossing with Bouscat Giant Flemish Giant Havane Rex INRA 1027 INRA 1077 INRA 1089 Coloured Dwarf		*Longissimus dorsi*	 5.75ab 5.71bc 5.77a 5.74ab 5.69c 5.73ab 5.73ab	 *						
NATH & RAO, 1985	Wild Rabbit (O. Hispidus) New Zealand White	adult	thigh	6.33 6.13	**	1,68 1,88	**				
	Wild Rabbit (O. Hispidus) New Zealand White		shoulder	6.40 6.17	**	2.01 2.29	**				
MASOERO *et al.*, 1986	Terminal crossing with: Flemish Giant Burgundy Fawn Wien Blue New Zealand White Californian French Silver	average weight 2664 g	*Biceps femoris*	 5.86a 5.83ab 5.85a 5.76c 5.75c 5.77bc	 *						
RISTIC, 1986	Terminal crossing with: Zika Hyla	average of three ages (10,12,14 weeks)	loin (b)	 5.63 5.45	 **					 61.6 (c) 58.0	 * *
	Terminal crossing with: Zika Hyla		thigh (b)	 5.77 5.69	 **	 8.5 8.3	 ns	 25.7 25.1	 ns	 57.4 54.8	 *
BLASCO & PILES, 1990	Selected Strain A Selected Strain V	70 d	*Longissimus dorsi*	5.71 5.66	*						
	Selected Strain A Selected Strain V		*Biceps femoris*	5.82 5.77	*						

Table 2 : suite

DAVID *et al.*, 1990	Terminal crossing with: Flemish Giant INRA 9077 (a) Terminal crossing with: Flemish Giant INRA 9077 (a) Terminal crossing with: Flemish Giant INRA 9077 (a)	79 d	*Biceps femoris* *Semi membranosus accessorius* *Tensor fasciae latae*	5.84 5.85 5.91 5.88 5.91 5.89	ns ns ns						
RISTIC *et al.*, 1990	New Zealand White (NZW) Silver Giant (SG) NZW x SG SG x NZW	98 ± 5 d	thigh (b)	5.78 5.76 5.82 5.79	ns	8.5 8.9 8.5 9.1	ns	27.5 24.5 26.1 25.2	ns	51.4 (c) 52.4 55.1 58.2	* *
RISTIC & ZIMMERMANN, 1992	Zika Terminal crossing with: Zika Hyla Zika Terminal crossing with: Zika Hyla	average of two ages (77, 84 d)	loin (b) thigh (b)	5.59 5.72 5.42 5.74 5.87 5.65	** **	 8.4 7.7 8.4	 ns	 23.7 25.3 24.6	 ns	50.9 (c) 62.9 55.8 62.4 60.5 54.7	* *
PERRIER & OUHAYOUN, 1993	Terminal crossing with: Zika INRA 9077 (a)	average of two ages (84, 91 d)	average of three thigh muscles	5.68 5.63	**			24.1 24.1	ns		
BATTAGLINI *et al.*, 1994	Terminal crossing with: White Giant Heavy Strain Grimaud Light Strain Grimaud	average of two ages (75, 90 d)	*Longissimus dorsi*	5.67a 5.73b 5.71ab	*	35.7 35.7 35.6	ns	33.4 33.5 34.4	ns	57.1 (d) 57.6 57.1	n s
NIEDZWIADEK *et al.*, 1996	New Zealand White Californian Termonde White	90 d	leg	6.00 6.00 5.98	ns						
LAMBERTINI *et al.*, 1996	Provisal Hyla Provisal Hyla Provisal Hyla	average of three ages (65, 85, 95 d)	*Latissimus dorsi* *Biceps femoris* *Soleus*	6.16 6.14 5.87 6.03 6.76 6.73	ns ns ns						

(a): unselected control strain
(b): thawed sample
(c): Göfo system
(d): CIE L*a*b* system
(e): water holding capacity is generally determined according to GRAU & HAM (1957): area of expressed fluid to area of meat, or inversely
ns: non significant (P > 0.05)
*: significant (0.01 < P < 0.05)
** highly significant (P < 0.01)
values with different superscript differ significantly (P < 0.05)

2.1.3.3. rate in reaching a fixed weight

CABANES-ROIRON and OUHAYOUN (1994) compared two lots of animals slaughtered at the same weight, which was reached at either 62 or 73 days. The older rabbits have the stronger body maturity characteristics (high slaughter yield and meat to bone ratio), probably in relation to a lower adult body weight. In spite of their greater presumed weight maturity, which should be accompanied by a more glycolytic muscular metabolism, the average pHu of the muscles is higher. The authors suggest that pHu has a genetic determinism independent of growth parameters, especially adult body weight.

Uneven muscle development, analysed by VÉZINHET *et al.*, (1972), is thus a contributory factor in the variability of muscular pHu in young animals. The range of muscles studied and the interaction of growth parameters (age, weight, and degree of maturity) make the interpretation of results difficult. However, it seems that pHu diminishes with age (and weight) as a result of an increase in glycolytic metabolism. This variation, which depends on the precocity of muscle development, ceases between 4 and 10 weeks.

2.1.4. Genetic factors

2.1.4.1. Sex

Sexual dimorphism of ultimate pH does not seem to exist (OUHAYOUN *et al.*, 1974; NIEDZWIADEK *et al.*, 1983; RISTIC, 1986-1989; RISTIC *et al.*, 1990; KROGMEIER and DZAPO, 1991; PARIGI-BINI *et al.*, 1992; GRASHORN *et al.*, 1996), and neither does any enzyme activity specific to the main muscular energy metabolism pathways (BACOU and VIGNERON, 1976a). However, MASOERO *et al.*, (1986) find a lower pHu in females, whereas LAMBERTINI *et al.* (1996) find the opposite, at least in the *Latissimus dorsi* muscle.

2.1.4.2. Breeds, strains and crosses

Since 1974, at least fifteen authors have studied the variability of muscular pH and related traits between genetic types. Four studies relate to the pH levels in the first moments after slaughter. Interpretation of the results of CHIERICATO *et al.* (1996), who looked at the average pH taken 3 hours and 24 hours *post mortem*, is difficult. This is also true for the work of BLASCO and PILES (1990) and BATTAGLINI *et al.* (1994), which concern the differences between pH measured in the hour after slaughter and ultimate pH. In fact, the kinetic of initial muscle acidification, which is very rapid, and the lack of available water in the muscle when the pH is around neutral, do not permit very precise or repeatable pH measurements *in situ*. Ninety minutes after slaughter, KROGMEIER and DZAPO (1991) observed a difference in muscular pH between the New Zealand White and Silver Giant breeds and a lower value in the respective crosses of these two breeds; they attribute these findings to the heterosis effect (-2.6%).

pH measures mostly concern ultimate values (pHu) (Table 2). It is well known that pHu variations between muscles are determined by glycogen reserves, depending on muscular fibre typology, which changes during growth (Cf. § 2.1.1 to 2.1.3). Do the variations in pHu observed between breeds, strains and crosses depend on the same fundamental effects: fibre typology and stage of development ?

In the rabbit species, which is characterised by a wide variety of adult form, breeds are less precocious the larger their adult size. For example, at the age of 11 weeks, the degree of weight maturity (percentage of adult weight) of terminal rabbits is 75% when the sire is of the Dwarf Coloured breed (adult weight: 1.7 kg) and 57% when the sire is of the Flemish Giant breed (adult weight: 5.3 kg) (OUHAYOUN, 1978). Are these differences in *weight* precocity accompanied in the musculature by differences in *metabolic* precocity and consequently differences in ultimate pH ?

Published informations are contradictory. The Small Russian breed (adult weight: 2.8 kg), which is more precocious from a weight point of view than the New Zealand White breed (adult weight: 3.7 kg), is characterized by a more rapid diminution in oxidative energy metabolism during growth (OUHAYOUN *et al.*, 1983). The higher muscular pH in rabbits of the large sized Zika strain compared to the New Zealand White (PERRIER and OUHAYOUN, 1993) or Hyla (RISTIC, 1986; RISTIC and ZIMMERMANN, 1992), may also be attributed to their lower developmental precocity.

But the relationship between weight precocity and metabolic precocity is not confirmed in the comparison, at the same age (consequently, at various degree of maturity), of crossbred from of extreme size sires such as Flemish Giant and Coloured Dwarf. The former, the least precocious, demonstrates a more glycolytic (aldolase / ICDH ratio) muscular energy metabolism (OUHAYOUN, 1978), the result of a fibre typology which favours type αW (VIGNERON and BACOU, 1976). It should be noted that, paradoxically, these enzymatic and typological differences do not translate into differences in ultimate pH (OUHAYOUN, 1978). The absence of logical links between the metabolic and typological characteristics of meat and the pHu of meat is not unusual. Thus LAMBERTINI *et al.* (1996) demonstrate that the higher levels of βR and αR fibres in Hyla strain rabbits, compared with Provisal strain rabbits, have no effect on the ultimate pH of meat.

It appears that the differences between breeds and crosses in muscular characteristics are attributable either to differences in development or to a genetic determinism that is independent of adult form. The

muscular characteristics of the wild rabbit (*Oryctolagus hispidus*) certainly show evidence of the second instance. In fact, compared to the heavier, less precocious New Zealand White breed, the wild rabbit is characterised by both a high pHu (NATH and RAO, 1985) and a high percentage of βR and αR fibres (VIGNERON and BACOU, 1976; KULISKOVA *et al.*, 1985).

The relationships between ultimate muscular pH and meat quality traits (WHC and colour) are not well documented. Even though their pHu is different, the muscles of Hyla and Zika hybrids have the same water holding capacity and the same cooking loss; but they are differentiated by their brightness. The latter is lower (high Göfo values) in the less acid pH muscles of the Zika hybrid (RISTIC, 1986 ; RISTIC and ZIMMERMANN, 1992). But this pHu / brightness relationship is not observed in pure breeds (RISTIC and ZIMMERMANN, 1992). The significant effects on pHu found in comparisons of genetic types by PERRIER and OUHAYOUN (1993) and BATTAGLINI *et al.*, (1994) are not found in characteristics that are logically correlated. With equivalent pHu levels, the muscles of New Zealand White and Silver Giant breeds and their reciprocal crosses are differentiated by their brightness. The lowest levels are seen in the Silver Giant and especially in the crossbreeds (RISTIC *et al.*, 1990), which could be attributed to a heterosis effect.

2.1.4.3. Intra-genetic-type variability

An estimation of the genetic parameters of growth performance and ultimate muscular pH has been made on the basis of data collected during trials on the performance of the offspring of certain male lines (OUHAYOUN *et al.*, 1973, 1974; WALCKIERS, 1973, RAGOIS, 1974, VRILLON *et al.*, 1979). When the selection of male lines for growth rate first started, it was important to know its impact on meat quality. Muscular pH was measured *in situ* by inserting pH electrodes into the *Biceps femoris* or *Longissimus dorsi* muscles. Analysis of myoglobin, which takes longer, was done *in vitro* using samples from the *Abdominis transversus* muscle. Estimations of genetic parameters were made using terminal crossed rabbits - 279 in number for muscular myoglobin levels and 5012 for muscular pH (Table 3).

According to the estimations, the heritability (h^2) of growth rate between the ages of 28 and 70 days (the selected trait of sires) lies between 0.36 and 0.60. For carcass weight, h^2 lies between 0.11 and 0.60. For ultimate pH, h^2 lies between 0.11 and 0.72, according to the estimations and to the analysed muscles. The heritability of myoglobin content lies between 0.29 to 0.56. Finally, the heritability of chilling water loss of carcasses (2°C, 24 hours) is estimated at 0.18.

The positive genetic correlation of pHu and myoglobin content of muscle ($0.44 < r_G < 0,69$) is

Table 3 : Heritabilities (diagonal) and genetic correlations of growth performance and meat traits.

		6	5	4	3	2	1
Chilling carcass water loss	**(1)**	-0.30 (c)	-0.55 (c)	-0.87 (c)	0.17 (c)	0.70 (c)	0.18 (c)
Carcass weight	**(2)**	-0.09 (c)	-0.37 (c)	-0.79 (c) -0.75 (a) -0.26 (e) -0.56 (d)		0.11 (a) 0.60 (d) 0.36 (e)	
Growth rate	**(3)**	-0.08 (c) -0.35 (b)	-0.42 (c)	-0.22 (c) -0.47 (a) -0.05 (e) -0.55 (d)	0.36 (a) 0.44 (e) 0.60 (d)		
***Biceps femoris* ultimate pH**	**(4)**	0.69 (c)	0.88 (c)	0.11 (c) 0.50 (e) 0.72 (d)			
***Longissimus dorsi* ultimate pH**	**(5)**	0.44 (c)	0.20 (c)				
***Transversus abdominis* myoglobin rate**	**(6)**	0.29 (c) 0.56 (b)					

(a) OUHAYOUN *et al.*, 1973 / (b) WALCKIERS, 1973 / (c) RAGOIS, 1974 / (d) OUHAYOUN *et al.*, 1974 / (e) VRILLON *et al.*, 1979

Figure 6 : New Zealand White and Californian rabbits in fattening wired cages (photo OUHAYOUN)

indicative of the opposition that exists between the two main energy metabolism pathways.

The genetic correlation (r_G) of growth rate and pHu lies between -0.05 and -0.55; and that of growth rate and myoglobin levels between -0.08 and -0.35. The selection of terminal crossing sires on the growth rate performance of their offspring may therefore entail a lowering of the oxidative pathway for muscular energy metabolism in favour of the glycolytic pathway. The negative genetic correlation of chilling water loss and pHu ($-0.55<r_G<-0.87$) or myoglobin content ($r_G = -0.30$) are already indicative of a possible degradation in meat quality as a result of selection for growth rate.

It should be noted that pH measured 30 minutes after slaughter (pH_{30}), in order to estimate the rate of muscular acidification, shows a comparable heritability to that of pHu (0.33 and 0.29 for the *Longissimus dorsi* and *Biceps femoris* muscles respectively). However, whereas the genetic correlation of pHu and myoglobin levels is positive, that of pH_{30} and myoglobin levels is negative (high myoglobin levels, more oxidative metabolism, rapid fall in pH) (RAGOIS, 1974). This genetic antagonism is more pronounced in the *Biceps femoris* muscle ($r_G = -0.74$) than in the *Longissimus dorsi* muscle ($r_G = -0.38$) (the latter is more glycolytic) and is probably due to the fact that, in families with muscles higher in αR fibres (oxydo-glycolytic) and better irrigated, the glycolytic action of catecholamins liberated during electroanaesthesia is more pronounced.

Published material does not indicate differences between breeds in muscular pHu above 0.23 units. Consequently, the genetic variability between breeds of technological meat characteristics, usually correlated to pHu, is low. In the rabbit species, therefore, there are no breeds that present abnormal acidification kinetics or ultimate pH, as exist in pigs (MONIN, 1988), which can determine qualitative defects in meat.

In spite of the existence of differences between estimated intra-breed genetic parameters for muscular pH and its correlated traits, the results of bibliographic analysis are coherent. The heritability value of pHu makes this trait an effective indicator of muscular energy metabolism and meat quality. The negative genetic correlation between pHu and growth rate indicates that muscular pH has to be taken into account in selection programmes for weight productivity. The risk of acid meat appearing in high growth potential strains would then be avoided.

2.2. EFFECT OF DIETARY FACTORS

For maximum meat production, the equilibrium recommended for a diet fed *ad libitum* are the following: 10.45 MJ kcal digestible energy/kg, 15 to 16% raw proteins or better still 11 to 11.5g of digestible proteins/MJ of digestible energy, 13 to 14% raw cellulose and a lipid content of about 3%. Any substantial variation in these feeding conditions may modify the growth rate, the anatomical equilibrium of the carcass and the composition of the edible fraction, i.e. the amount of meat produced and its quality (OUHAYOUN *et al.* 1985-86, OUHAYOUN, 1991-92) (Figure 6)

2.2.1. Feeding levels

Feed restriction, whether devised to reduce feed costs or to modify body composition, can have an effect on the muscular metabolism, in so far as it slows down general growth rate. For example, a moderate limitation in access to feed (six to ten hours a day) for fattening rabbits between 6 and 14 or 18 weeks has no significant effect on growth rate nor on the technological meat properties (pH, colour, WHC, cooking loss) (OSMAN, 1991). However, as soon as the amount of feed offered falls below 85% of *ad libitum* intake, feed efficiency is lower and growth rate slows down (OUHAYOUN *et al.* 1985-1986). Depending on the level of feed restriction and the time of application, the reduction in growth rate is allied to modifications to the allometry of tissue and organ growth and thus to carcass quality. ASGHAR *et al.*, (1981) tested extreme feed restriction situations between the ages of 30 and 50 days: *ad libitum* feeding allowing normal growth, restricted energy supply of 70 and 83% leading to either maintenance of the initial weight or weight loss. Muscular pHu is then clearly affected (5.67, 5.83 and 6.24 respectively). Even when the feed restriction leads to a reduction in sarcoplasmic proteins in the musculature, and thus theoretically (SCOPES, 1970) in the activity of the glycolytic energy metabolism pathway, the authors attribute the rise in pHu solely to the reduction in glycogenic muscular reserves. Return to normal feeding levels brings about a

compensatory growth, so that at 80 days, the three lots of rabbits achieve the same weight and a common muscular pHu (5.65). For PERRIER and OUHAYOUN (1996), feed restriction (35-56 days) followed by *ad libitum* feeding (56-77 days) leads to better growth rates between 35 and 77 days than the inverse sequence, with the rabbits consuming the same quantity of feed over the 42 days fattening period. The muscular tissue of rabbits given the more abundant finishing diet, which exhibited a strong compensatory weight gain, have a more acid pHu (5.73 *vs* 5.77), which may be attributed to stimulation of the glycolytic pathway for muscular energy metabolism (DALLE ZOTTE and OUHAYOUN, 1995).

2.2.2. Fibre content

In trials on the utilisation by rabbits of raw materials high in parietal carbohydrates, an increase in the proportion of bulky feeds in the diet can have comparable effects on muscular tissue to those of feed restriction. Thus GIERUS and ROCHA (1997) demonstrate that increasing forage level in the diet (0, 15 and 45 %), does not affect overall protein and energy levels (sic), nor growth rates between weaning and 2 kg in weight, but entail a reduction in muscular glycogenic reserves and a corresponding rise in their pHu. In the *Semimembranosus accessorius* muscle, for example, pHu values are 5.60, 5.69 and 5.85 respectively.

2.2.3. Lipid levels

The classic means of achieving optimal digestible energy levels in a diet rich in bulky feeds is to supplement with plant or animal fats. According to RAIMONDI *et al.* (1975), the addition of lipids to the diet (4 or 8%) during the finishing period (10 to 13 weeks) gives the muscles a higher pHu (6.00 *vs* 5.80 in the *Biceps femoris*) than in rabbits given the same lipid supplementation in the early stages of fattening (5 to 10 weeks). Contrary to all expectations, the high pHu of the muscles is correlated to low water retention during cooking. PLA and CERVERA (1996) and ANGELS OLIVER *et al.* (1997) also demonstrate that supplementing the diet with lipids between 30 and 65 days has no effect on the growth rate, but does affect muscular pHu, especially if the fats are of animal origin. In this case, the pHu of the *Longissimus dorsi* muscle increases from 5.66 to 5.76. The increase in pHu is accompanied by an improvement in WHC in raw and cooked meat and a reduction in cooking loss. The brightness of the meat does not change. This rise in muscular pHu can be attributed to the fact that the immediate availability of acetic acid, derived from the ingested fatty acids, favours the metabolism of αR fibres, which have an enzymatic oxydo-glycolytic potential.

2.2.4. Nitrogen levels

At a constant level of digestible energy, increasing the protein level (10.4, 13.8, 17.2%) in feed given to fattening rabbits (4 to 11 weeks) improves growth rates and at the same time increases the sarcoplasmic fraction of muscular nitrogen and the activity of the glycolytic channel of energy metabolism (OUHAYOUN and DELMAS, 1983). Rabbits selected for growth rate and farm rabbits react in the same way. Corresponding variations in the activity of the glycolytic metabolic pathway and the level of sarcoplasmic proteins are attributable to the fact that 70% of the latter are involved in the glycolytic process. Given the correlation between muscular glycolytic activity and pHu (DALLE ZOTTE and OUHAYOUN, 1995), it is probable that pHu is more acid in rabbits being fed a more protein rich diet.

Some studies have dealt with the quality of the nitrogen fraction in the diet of rabbits. Substituting proteic nitrogen with urea has been tested with success (NIEDZWIADEK *et al.*, 1975). But at the rate of 2%, it slows down growth rate without affecting the technological properties of the meat (pHu, WHC, colour). Supplementation with lysin and/or methionin of feeds at 16% crude protein and with lysin of feeds at 20 or 22% crude protein has no effect on the pHu of meat nor on normally correlated traits (WHC, colour) (CZAJKOWSKA *et al.*, 1980a, 1980b).

2.2.5. Growth factors

Supplementation of feed with β adrenergic agonists improves the growth rate in rabbits, favours nitrogen retention and limits the amount of fat cover. Clenbuterol, in particular, added to the fattening diet at the rate of 100 mg per day, between the ages of 70 and 98 days, leads to a definite increase in muscular pHu (+0.3 pH unit), with a corresponding reduction in weight loss during cooking. The increase in pHu is due to stimulation of the oxidative metabolism (aldolase / ICDH ratio) and a reduction of muscular carbohydrate reserves (HULOT *et al.*, 1996).

Studies of the relationships between dietary factors and pHu have been relatively few. The level of feeding and nutrient balance affects muscular energy metabolism and meat properties. A high level of proteins in the diet, intended to increase growth rate, favours the glycolytic pathway for metabolising muscular energy and consequently entails a lowering of meat pHu. Conversely, supplementing the diet with lipids or parietal carbohydrates, as well as feed restrictions, slows down growth rate and increases meat pHu.

Table 4 : Research state on rabbit meat technology

	Ante mortem treatment		Slaughtering	*Post mortem* treatment		Meat processing	
	Fasting	Transportation	Stunning	Electrical stimulation	Chilling	Storage	Deep freezing
BATE-SMITH and BENDALL, 1949	*		*				
LOCKER and HAGYARD, 1963					*		
LAWRIE, 1968 b					*		*
COSTANTINI and BOSI, 1968						*	
SCHEIBNER, 1970					*	*	
HENDERSON *et al.*, 1970					*		
BENDALL, 1973 a					*		
BENDALL, 1973 b					*		
BENDALL, 1976				*			
SENESI *et al.*, 1975						*	*
SENESI *et al.*, 1976						*	*
GEY and THORMANN, 1978		*					
SUNKI *et al.*, 1978						*	
PARISI *et al.*, 1979						*	
IKEUCHI *et al.*, 1980					*		
MEYER-RAVEINSTEIN *et al.*, 1980						*	
KANG *et al.*, 1983				*			
JOLLEY *et al.*, 1983					*		*
HYUN and CHOE, 1984				*			
HORGAN and KUYPERS, 1985				*			
GARIEPY *et al.*, 1986						*	
ITO *et al.*, 1986					*		
OUHAYOUN, 1988		*	*		*		
JIN and PARK, 1988				*			
OUHAYOUN and DELMAS, 1988					*		
OUHAYOUN *et al.*, 1989					*	*	
CIVERA *et al.*, 1989			*				
DELMAS and OUHAYOUN, 1990					*		
OUHAYOUN and POUJARDIEU, 1990			*		*		
OUHAYOUN *et al.*, 1990 a					*		
OUHAYOUN *et al.*, 1990 b					*		
JOLLEY, 1990	*	*					
KANG *et al.*, 1991				*			
JOO *et al.*, 1991				*			
MASOERO *et al.*, 1992	*	*					
XICCATO *et al.*, 1994		*					
HADDAD *et al.*, 1994 a					*		
CABANES-ROIRON *et al.*, 1994						*	*
CABANES *et al.*, 1995						*	*
OUHAYOUN and LEBAS, 1995	*	*	*				
CABANES *et al.*, 1996						*	*

2.3. INFLUENCE OF TECHNOLOGICAL FACTORS

During the time when the farmer begins to prepare the rabbits for the slaughterhouse to the time when the consumer prepares the meat, several important events occur, which vary in scope and duration. In chronological order these are: 1- loading the rabbits, their transport, sometimes for hundreds of kilometres, possibly followed by a period of rest at the abattoir; 2- slaughtering, which is dominated by the stress of

electroanaesthesia; 3- immediate or deferred chilling of the carcass which is sometimes preceded by electrostimulation; 4- storage of the meat in the commercial network, where there can be breaks in the continuity of refrigeration. Freezing may be used at times of seasonal surplus production. This can produce negative effects, such as "thaw *rigor*", if the meat is frozen before the onset of *rigor mortis*. The cumulative and / or interactive effects of these variation factors on the pH of meat and its correlated traits can be important. Since the 1950s, a lot of applied and cognitive literature has been published on this subject (Table 4).

2.3.1. *Ante mortem* treatment

The stress to which the rabbit is subject at collection, during transport and just before slaughter is evident in catecholamins release, muscular contractions and rise in body temperature, whole events that contribute to accelerate glycogenolysis *in vivo*.

At the moment of death, the animal may have exhausted all or some of its energy reserves, which limits the extent of *post mortem* acidification. In experimental conditions, the injection of adrenaline 4 hours before slaughter accelerates the rate of acidification (0.32 *vs* 0.24 pH units per hour), but limits its extent (6.48 *vs* 5.70) (BENDALL and LAWRIE, 1962). Some intense, experimentally applied stresses bring about a depletion of glycogen to the extent that pHu is equal to initial pH and the conditions of *rigor mortis* onset are profoundly modified (BATE-SMITH and BENDALL, 1949).

2.3.1.1. Fasting

The muscles of rabbits deprived of food for 48 to 72 hours have a high pHu (BATE-SMITH and BENDALL, 1949). The rise in pHu, from the 24th hour of fasting, is due to a depletion of glycogenic muscle reserves (JOLLEY, 1990). This depletion is correlated with an increase of WHC and a decrease in brightnesse of the meat, even in rabbits submitted to a short (17 hours) hydric diet (OUHAYOUN and LEBAS, 1995). The findings of MASOERO *et al.* (1992) that fasting diminishes muscular pHu is an exception.

2.3.1.2. Transport

Transport lasting 24 hours causes a significant rise in pHu in the *Biceps femoris* muscle (6.27 *vs* 5.90) (JOLLEY, 1990). According to MASOERO *et al.* (1992) and XICCATO *et al.* (1994), two hours in the lorry are enough to cause a significant rise in pHu. OUHAYOUN and LEBAS (1995) estimate that pHu in the *Longissimus dorsi* and the *Biceps femoris* is 0.2 units higher in rabbits transported for 250 km than in those transported for only 30 km. The transport effect is more pronounced than the effect of fasting and is due to the depletion of glycogenic muscle reserves. JOLLEY (1990) finds that these reserves pass from 15.5 to 8.23 µmoles of glucose per gram of muscular tissue during a 24-hour journey. They can be partially restored by resting. Thus a rest period of 18 hours after 250 km of transport lowers pHu from 5.81 to 5.72 (OUHAYOUN and LEBAS, 1995). This restoration of muscular energy reserves is attributable to the mobilisation of glycogen in the liver, which had accumulated (glycogenogenesis) while the animal was exhausted. The rise in pHu during transport is accompanied by an improvement of WHC in the *Biceps femoris* muscle (JOLLEY, 1990), a greater ability of the carcass to absorb water during pre-freezing soaking (GEY and THORMANN, 1978), a reduction in cooking loss (XICCATO *et al.*, 1994) and a reduction in brightness (JOLLEY, 1990; XICCATO *et al.*, 1994; OUHAYOUN and LEBAS, 1995). All these characteristics are those of DFD meat (dark, firm, dry), but without its excesses. Rheological and sensory tests on meat give conflicting results, according to OUHAYOUN and GILBERT (unpublished data) and XICCATO *et al.* (1994), meat quality is improved, whereas according to MASOERO *et al.* (1992) meat quality is reduced..

Ante mortem treatments such as a hydric diet and transport, which entail long-lasting stress, have noticeable effects on rabbits. They lead to dark meat, whose high pH favours the development of putrefaction bacteria. A short transport, leading to only a small rise in pHu, improves the taste, tenderness and juiciness of meat.

2.3.2. Slaughtering

Slaughtering is an extremely violent stress whatever method is employed. BATE-SMITH and BENDALL (1949) have clearly demonstrated this by giving or withholding tranquillisers (myanesin) before slaughter. Muscle of tranquillised rabbits, incapable of experiencing stress, had a higher pH level measured 5 minutes *post mortem* than stressed animals (7.0 *vs* 6.5) (Figure 7).

Several methods are used to stun rabbits before bleeding. Dislocation of the neck is now only used in small-scale operations. Electroanaesthesia is the legally recommended method: low voltage electrocoma (<100V, 50Hz) or electroshock (up to 320 V, 50 Hz). These techniques engender a tetany of the entire musculature, an almost instantaneous rise in muscular temperature of around 1° and an intense secretion of catecholamins. Compared to dislocation, electrocoma accelerates the fall in pH of the *Longissimus dorsi*, with a dominant glycolytic energy metabolism, but tends to slow it down in the thigh adductor, which is a more oxidative muscle. The WHC of muscles is not affected by the mode of stunning in the *Longissimus dorsi*, but it is improved by electrocoma in the thigh adductor (OUHAYOUN, 1988). Electroshock provokes a low-grade and transient

shortening of the sarcomeres in the musculature (OUHAYOUN and POUJARDIEU, 1990). CIVERA *et al.* (1989) compared several stunning methods (electric shock 12volt 4 seconds, 24 volt 2 seconds, vertebral dislocation, mechanical shock); electric stunning entails the fastest drop in pH, both in *Psoas major* and *Longissimus dorsi*. pHu is not affected by the stunning method.

The stress of electroanaesthesia accelerates muscular acidification, leads to a transient shortening of the sarcomeres, but does not modify ultimate pH in the meat.

2.3.3. Post mortem treatment

2.3.3.1. Electrical stimulation of carcasses

In rabbits, carcass stimulation increases the rate at which pHu is reached, but does not modify it (BENDALL, 1976; KANG *et al.*, 1983; HYUN and CHOE, 1984; HORGAN and KUYPERS, 1985; JIN and PARK, 1988; JOO *et al.*, 1991). This stimulation is applied at the carcass preparation stage. It accelerates acidification and depletion of muscular ATP and consequently is able to avoid the risk of "cold shortening" or "thaw *rigor*". By favouring muscular acidification, stimulation also improves the hygienic meat quality. This muscular acidification occurs in two stages. During stimulation, pH lowers by around 0.3 units, whatever the length of the stimulus (BENDALL, 1976) or the intensity (HORGAN and KUYPERS, 1985) of the current applied. After stimulation, the acidification rate is closely linked to the type of electric shock. After an electric shock of 250 volts and 15 Hz for 120 seconds, the pH fall and the ATP hydrolysis are two to three times faster in the *Longissimus dorsi, Biceps femoris* and *Triceps brachii* muscles than in a non-stimulated control; a 14 second stimulation has no effect (BENDALL, 1976). HORGAN and KUYPERS (1985) confirm that high-tension shocks are more effective at unleashing the post-stimulation effects. Finally, the onset of *rigor mortis*, estimated by measuring the extensibility of the *Psoas major* muscle, is faster (5 hours *vs* 7-8 hours) after a high-tension stimulation than after a low-tension stimulation (KANG *et al.*, 1991). All of these physico-chemical phenomena together result in a degradation of WHC (JIN and PARK, 1988, JOO *et al.*, 1991).

2.3.3.2. Carcass chilling

For reasons of hygiene, carcasses should be chilled rapidly (Figure 8). Chilling occurs at the critical period of *rigor mortis* onset, which is characterised by the progressive loss of muscular elasticity and by its acidification.

Cold (0°C *vs* 37°C) slows down the physico-chemical processes of *rigor mortis* in the *Longissimus dorsi* muscle; in particular, it reduces the rate at which pHu is reached (IKEUCHI *et al.*, 1980) (Figure 9) and the intensity of sarcomeres contraction (HENDERSON *et al.*, 1970). For the first three hours of chilling, the rate of acidification is much slower at 2°C than at 12°C (0.19 *vs* 0.13 units of pH per hour) (OUHAYOUN *et al.*, 1990 a). Consequently, at the end of this period, the energy potential in the rapidly refrigerated (2°C) muscles is higher (OUHAYOUN *et al.*, 1990b).

Helding the carcasses at room temperature (14°C) before chilling (2°C) favours muscle acidification, through an acceleration of energy reserves depletion, but does not influence the ultimate pH of muscle (22 h *post mortem*), which is depending more on the muscular energy reserves at the moment of slaughter than on the conditions under which they are used up. Thus after 5 hours of chilling, the highest muscular pH (6.05 *vs* 5.89)

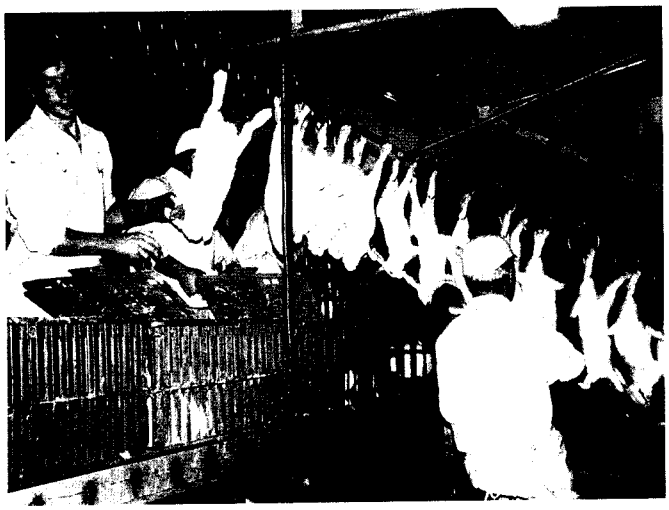

Figure 7 : Hanging and bleeding of rabbits in an industrial slaughterhouse (photo OUHAYOUN)

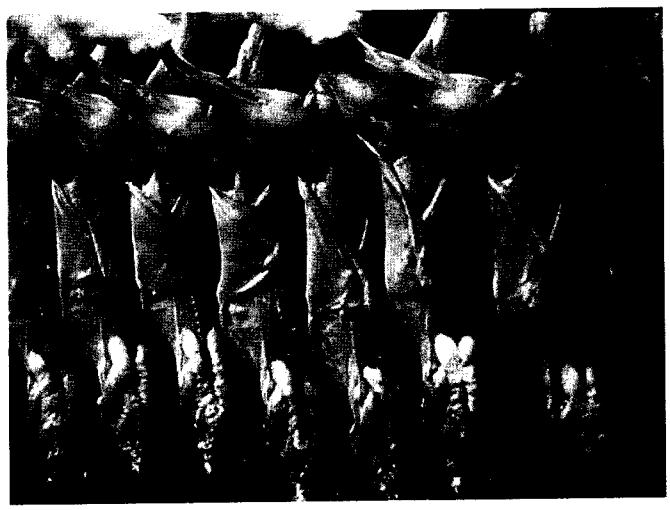

Figure 8 : Chilled rabbit carcasses in an industrial slaughterhouse (photo OUHAYOUN)

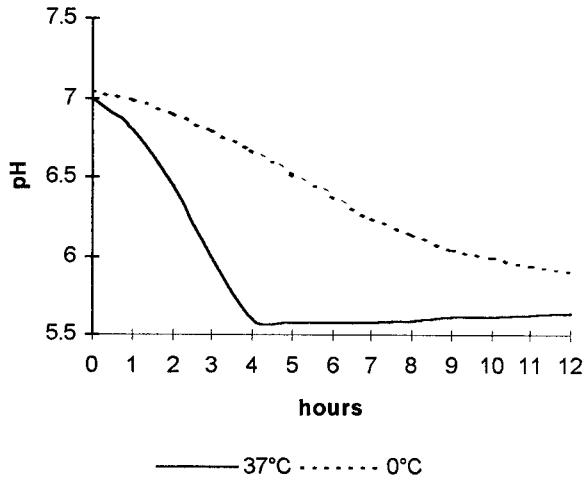

Figure 9 : *Post mortem* acidification in rabbit muscle at 0° and 37°C (after IKEUCHI *et al.*, 1980)

is found in carcasses which have been kept the shortest (13 *vs* 54 minutes) at room temperature (OUHAYOUN *et al.*, 1989). According to these authors, if the carcasses are pre-packed after a brief chilling (i.e. 5 hours) occurring shortly after slaughter (i.e. 13 minutes), the large following acidification of muscle in the package is linked with the development of a surface humidity during storage, which may prejudice the hygienic quality of meat.

Chilling of muscular tissue therefore entails a slowing down of the physico-chemical phenomena, except when "cold shortening" develops. This phenomenon is often encountered in cattle and sheep and occurs when carcasses are subject to severe chilling *ante rigor*.

Rabbit carcasses are light and lack an insulating adipose tissue. Even when chilling parameters are moderate (air at 5°, speed 0.3 m/s, hygrometry 70%), the temperature at the centre of the meat is down to 7°C in less than 2 hours (OUHAYOUN and DELMAS, 1988). The general physico-chemical conditions of "cold shortening" are then grouped together (Cf § 1.2.1). Muscles with an oxydo-glycolytic metabolism (rich in αR fibres), whose ATPasic systems are not inhibited by cold and which acidify slowly, are theoretically more susceptible.

Several studies deal with this phenomenon in rabbits, taking into account two main manifestations: the shortening of the sarcomeres and the biochemistry of *rigor mortis*.

Based on measuring the sarcomere or muscle length, different muscles are revealed as more or less susceptible to "cold shortening". The *Semitendinosus*, an oxydo-glycolytic muscle, is susceptible (LAWRIE, 1968b; BENDALL, 1973b; LOCKER and HAGYARD, 1963). In the *Tensor fasciae latae*, the *Biceps femoris*, the *Gracilis*, which are also oxydo-glycolytic, there is no large-scale shortening of the sarcomeres by chilling (5 to 7%); it is partially inhibited by hanging the carcasses during chilling (OUHAYOUN and POUJARDIEU, 1990). The susceptibility of the *Longissimus dorsi*, a muscle whose fibre typology varies along an anterior - posterior gradient, is disputed; significant for JOLLEY *et al.* (1983) and OUHAYOUN *et al.* (1990b) and non-existent for HENDERSON *et al.* (1970), OUHAYOUN and POUJARDIEU (1990) and HADDAD *et al.* (1994a). The *Supraspinatus*, a slow, oxidative muscle, is not susceptible to "cold shortening" (OUHAYOUN *et al.*, 1990b). Only the last-mentioned authors observed a slight shortening of the sarcomeres by cooling in the *Psoas major*, a typically glycolytic muscle.

Using physico-chemical measures, ITO *et al.* (1986) observed accelerated ATP depletion and *rigor mortis* onset at 0°C; they attribute these anomalies in the physico-chemical processes to the re-release of Ca^{++} by the sarcoplasmic reticulum and to "cold shortening". OUHAYOUN *et al.* (1990a) had demonstrated that the fall in pH was noticeably slower at 2°C than at 12°C. However, OUHAYOUN *et al.* (1990b) observed that the slowing down of acidification and depletion of muscular energy reserves (ATP, glycogen) by cooling was less pronounced in muscles with an acid pH than in muscles with a moderate or high pH. This suggests that an anomaly in energy metabolism exists at low temperature in the more glycolytic muscles. In fact, if rapid chilling can entail a sarcomere shortening in certain muscles, the shortening is too small to provoke a toughness of the meat (HADDAD *et al.*, 1994a).

The effects of cooling on rabbit muscle has been the subject of little applied research. It is nevertheless a determining factor in the *rigor mortis* onset. Muscle chilling immediately after slaughter slows down all the physico-chemical phenomena of *rigor*: depletion of energy reserves, acidification, shortening of the sarcomeres. In spite of the ambiguity of certain experimental results, the phenomenon of "cold shortening" is not of major significance in rabbits. Consequently, the large amount of research into the electrical stimulation of carcasses is of only general interest.

2.4. MEAT PROCESSING

2.4.1. Refrigerated meat storage

All authors find that pH rises during the storage (2°C to 4°C) which follows chilling (COSTANTINI and BOSI, 1968; SCHEIBNER, 1970, CANTONI *et al.*, 1975; SUNKI *et al.*, 1978; PARISI *et al.*, 1979; MEYER-RAVENSTEIN *et al.*, 1980). It is accompanied by a rise in ammoniacal nitrogen levels (COSTANTINI and BOSI, 1968; SUNKI *et al.*, 1978; MEYER-RAVENSTEIN *et al.*, 1980). In skinned carcasses,

microbial pollution intensifies these changes (PARISI *et al.*, 1979). During storage for two weeks at 2°C, SENESI *et al.*(1976) found an increase in WHC, while pH tended to diminish.

The change in meat quality has been studied in different trial and error experimental situations, including the classic-factors (differed chilling, varying freezing durations, breaks in the refrigeration chain, etc..). pH only diminishes during cold storage if the preliminary chilling has been too short to allow muscular energy reserves to be exhausted. Thus during a 46 hour storage at 2°C, the pH of the *Longissimus dorsi* decreases by 0.34 units or rises by 0.05 units, depending on whether chilling lasted 5 or 21 hours respectively (OUHAYOUN *et al.*, 1989). During storage at 2°C for 12 days, the pH of the *Longissimus dorsi* rises from 5.81 to 5.91 up to 8 days and then stabilises at 5.88. This evolution may be attributed to two opposing mechanisms: a rise in the level of ammoniacal nitrogen (4.35, 9.05 and 13.81 mg/100 g respectively), which alkalinises the meat, and the production of free fatty acids, which tends to acidify it. Variations in WHC and brightness (L*) during storage are erratic. A break in the refrigeration chain (30 minutes at 20°C then 6 days at 7°C) increases pH levels in the *Longissimus dorsi* more than continuous storage at 2°C. This simulated incident has no effect on the deamination index, but it increases the acidity index. Bacterial proliferation makes the meat unfit for human consumption.

The pH of meat evolves differently under vacuum or in a modified atmosphere (100% nitrogen or carbon gas). After 50 days of storage, the lowest *Longissimus dorsi* pH was found in carcasses stored in a carbon gas atmosphere. In this atmosphere, microbiological qualities of meat are improved, but WHC is degraded, the meat is brighter, its toughness is increased (GARIEPY *et al.*, 1986).

When carcasses are stored at 2°C, the maturation process is evident in the rise of ammoniacal nitrogen levels and thus a rise in pH. If the chilling length before storage is only a few hours, continued muscular acidification in a confined atmosphere provokes the development of surface moisture on the meat, which is prejudicial to its keeping qualities. Any break in the refrigeration chain entails a rise in muscular pH and an active bacterial proliferation.

2.4.2. Deep frozen meat storage

To avoid a reduction in meat quality, freezing is done rapidly (-25°C), in the *post rigor* phase, when pH reaches its ultimate value (24 to 48 hours after slaughter). After storage (- 18°C) the cut should be thawed slowly (4°C). SENESI *et al.* (1975-76) reported that rabbit meat thawed after a storage period of one week to six months had a more acid pH than fresh meat (5.3 or 5.5 as against 5.9). CABANES-ROIRON *et al.* (1994) and CABANES *et al.* (1995-96), found that after 12 days at -18°C, the pH of the meat is more acid than that of meat kept refrigerated (2°C) for the same length of time (5.81 *vs* 5.88), but equal to that of fresh meat before treatment. During freezing, pH remains stable up to three months, then increases slowly; at 18 months, it reaches a slightly higher value than in fresh meat (5.71 *vs* 5.60 in the *Longissimus dorsi*, 6.02 *vs* 5.98 in the *Biceps femoris)*. As in the case of meat storage at 2°C, this alkalisation is attributable to the antagonistic effect of ammonia and fat free acid production. Whatever the length of storage, meat which has been frozen has a lower WHC than fresh meat (SENESI *et al.*, 1975; CABANES *et al.*, 1996). As to meat brightness, it appears to vary erratically during freezing.

If meat is frozen when it is still pantelant (*ante rigor*), "thaw *rigor*", which can occur on thawing, leads to an irreversible change in tenderness. "Thaw *rigor*" contraction is usually more intense than "cold shortening". For example, *Semitendinosus* muscle shows a shortening of the sarcomeres due to "thaw *rigor*" that was higher (39%) than that engendered by "cold shortening" (24%); *Psoas major* muscle, which resists to "cold shortening", demonstrated a 73% shortening of the sarcomeres during "thaw *rigor*" (LAWRIE, 1968b). This was observed despite high residual levels of ATP and phosphocreatin (BENDALL, 1973a). By measuring sarcomeres and the required shear force of the meat, JOLLEY *et al.* (1983) show that if *pre rigor* freezing is followed by thawing at 15°C, meat tenderness is not affected.

To avoid any reduction in tenderness as a result of "thaw *rigor*", meat should not be frozen before *rigor mortis* onset. Beyond a relatively short period when all muscular biochemical activity is blocked, storage of meat in frozen form does not entirely stop the maturation process, as is demonstrated by the rise in pH levels in the meat. The reduction in WHC of frozen meat is more a result of tissue lesions caused by the process of freezing and thawing than by variations in pH resulting from actual storage.

CONCLUSION

If measurements are taken under precisely controlled conditions, then pH is an extremely important indicator of the state of muscular tissue - both its metabolic equilibrium, which depends on growth parameters and genetic and dietary factors, and its physico-chemical evolution *post mortem* as a result of pre- and post- slaughter treatment. There are many studies of pH in rabbit meat, but the same is not true of correlated traits. WHC and fluid loss during cooking

the most frequently measured characteristics, are generally well explained by variations in muscular pH.

All factors capable of accelerating growth rate entail a lowering of pH, which is attributable to stimulation of the glycolytic energy metabolism pathway. This can be observed during periods of compensatory growth when normal dietary levels are re-established after feed restriction and when the fattening diet is very high in proteins. This is the predictable consequence of selection within a line for growth rate. By lowering WHC, a reduction in muscular pH is prejudicial to the sensory qualities of meat.

Slaughter conditions play an important role in the variation of pH and its ultimate value; fasting and transport, which cause a greater or lesser *ante mortem* depletion of energy reserves, particularly through the action of catecholamins, reduce the extent of acidification. The resulting meat is more alkaline and darker, with a good WHC, all qualities that improve sensory characteristics; but the storage qualities are compromised. Rapid chilling, which is implemented for reasons of hygiene, does not induce severe "cold shortening" in rabbits; it does not therefore reduce tenderness in the meat. Physico-chemical changes of the muscular tissue are slowed down by chilling. *Rigor mortis* is consequently differed, as is the achievement of ultimate pH.

When carcasses are kept in refrigerated storage and the refrigeration chain is not broken, the biochemical processes of maturation bring about a progressive rise in muscular pH. Storing meat in a frozen state reduces this evolution considerably, but does not stop it completely.

At the end of this review, it seems clear that the rabbit species does not present any anomalies in muscular acidification. There are no very high pH values, which could cause DFD meats, no abnormally low pH leading to acid meats and finally no sufficiently rapid acidification rates to result in PSE meats. This lack of susceptibility in rabbit meat does not however allow us to dispense with the proper precautions at all stages of production (selection, nutritional balance, technological treatment).

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