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MUSCULAR ENERGY METABOLISM AND RELATED TRAITS IN RABBIT. A REVIEW. (1)

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(1) This paper has been presented in the 5th Hungarian Rabbit Science Symposium (May 1993) ; it develops the part concerning rabbit of an academic interspecific work devoted to muscular energy metabolism written by Dalle Zotte (1992).

SUMMARY : After a brief reminder on the main stages of muscular differentiation, the paper gives a short account of some of the studies on the biology of muscles we have carried out on the rabbit and comments them in the light of results published in the world literature. Although subtile biological criteria are used, the aims of these works are highly practical. The objective is to better understand what determines variations in meat quality in the rabbit. It is now an evidence that the criteria which account for *post mortem* evolution of muscle into meat vary widely between muscles. The lasting character of metabolic differentiation explains the sensitivity of muscular traits and related technological criteria of meat to biological (somatotropin) or zootechnical (dietary nutrient balance, slaughter age) factors. The between and within breed variability of rate or/and amplitude of muscle differentiation has probably to be taken in account in programmes of genetic improvement of growth, in order to preserve meat quality.

RESUME: Métabolisme énergétique musculaire chez le lapin.
Après un bref rappel des principaux stades de la différenciation musculaire, cette revue résume nos travaux sur la biologie musculaire chez le lapin et les commente à la lumière des résultats parus dans la littérature mondiale. Bien que de fins critères biologiques soient utilisés, le but de ces travaux est essentiellement pratique. L'objectif est de mieux comprendre ce qui détermine les variations de la qualité de la viande de lapin. Il est maintenant évident que les critères qui concernent l'évolution post-mortem du muscle en viande varient grandement selon les muscles. Les conditions de la différenciation métabolique expliquent la sensibilité du muscle et des critères technologigues de la viande aux facteurs biologiques (somatropine) ou zootechniques (équilibre alimentaire, âge à l'abattage). Les variations entre races et intra-race de la vitesse et/ou de l'amplitude de la différenciation musculaire devraient probablement être prises en compte dans les programmes d'amélioration génétique de la croissance, dans le but de préserver la qualité de la viande.

INTRODUCTION

Muscle tissue accounts for two thirds of the carcass of rabbits slaughtered at 55 % of their adult weight. The aim of rational meat rabbit production is to obtain low cost muscle-rich animals yielding high quality meat. A sound knowledge of the biology of muscles should enable research workers to check whether these objectives are compatible and, if required, to optimize production methods so as to reconcile rearing productivity with meat quality. This question is tackled by giving general reminders on the biology of muscles and on the results of some of our studies on rabbit muscle tissue and meat.

MUSCLE TISSUE

1. Types of muscle fibres

As early as 1873 RANVIER claimed that variations in muscle colour within an animal are due to the existence of several types of muscle fibres. These fibres are nowadays classified according to two

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

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

criteria: contraction and relaxation speed, and main source of energy (ATP) used in contraction. Meat technologists usually use ASHMORE and DOERR's (1971) nomenclature when describing fibres. This classification recognizes three types of fibres: αR, αW and βR. Fibres can either be slow contracting (β type) or fast contracting (α type). This difference is due to the isoform composition of the myosin's heavy chains. The ATPase activity of the S1 heads of the myosin are inhibited at an alkaline pH in the first type and at an acid pH in the second. These properties make it possible to use histoenzymological techniques to discriminate between both types. The ATP used up by the muscle during contraction is regenerated by the oxidative and/or glycolytic pathways. The mitochondrial oxidative pathway uses acetic acid from several substrates (glycogen, glucose, fatty acids, amino acids) and produces water and carbon dioxide ; it is slow but highly energetic (34 ATP molecules per glucose unit). The sarcoplasmic glycolytic pathway breaks down glucose into lactic acid ; it is fast but not very energetic (3 ATP molecules per glucose unit). Fibres are classified into oxidative type (red = R) or glycolytic type (white = W) according to the relative importance of each pathway. The oxidative type can be histoenzymologically detected by checking for succinate dehydrogenase (SDH) activity.

Despite possible differences in diameter, all muscle fibres connected to the same motor unit are of the same contractile and metabolic types. These properties are described in table 1. Muscles, which include fibres of various types, are classified as white or glycolytic if they contain a high proportion of αW fibres, as red or oxidative if they mainly include αR and βR fibres and as mixed or oxido-glycolytic if their composition is intermediate.

2. Differentiation, development and growth

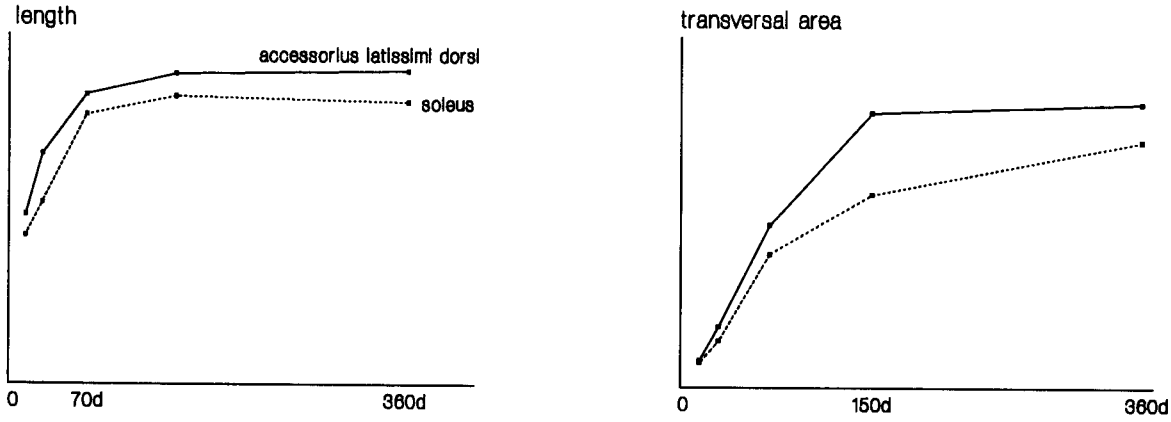
Muscle development occurs as a two-phase process: a cell proliferation phase and a morphological, functional and metabolic differentiation phase. Undifferentiated premyoblasts from the myogenic line (presumptive myoblasts) divide actively (hyperplasia) especially during the early stages of development. These cells then loose their capacity to undergo mitosis but acquire an ability to fuse. The fusion of myoblasts produces myotubes, i.e. elongated multinucleate cells whose nuclei, which are initially located in a central position, are gradually displaced towards peripheral areas by specific proteins. These stages of differentiation occur during early foetal life. However, the muscle tissue does retain some undifferentiated myogenic cells (satellite cells) which can fuse with the muscle fibres and thus increase the number of nuclei during their growth.

Morphological differentiation is followed by **functional differentiation**, which continues after birth in species with a short gestation period. The first generation of myotubes leads to slow muscle fibres. This is followed by a second generation of smaller myotubes which form the fast fibres of fast muscles and part of the slow fibres of slow muscles.

Metabolic differentiation occurs later than the differentiation into types of contraction. During the prenatal period fibres are moderately oxidative and very weakly glycolytic. All fibres are of the oxidative type at birth (αR or βR) and differences appear only later. αR fibres are then converted to αW fibres, the intensity and thoroughness of this conversion depending on how glycolytic the relevant muscles in the adult are. However, this conversion is reversible: exercising for instance increases the number of mitochondria in αW fibres and hence turns them into αR fibres.

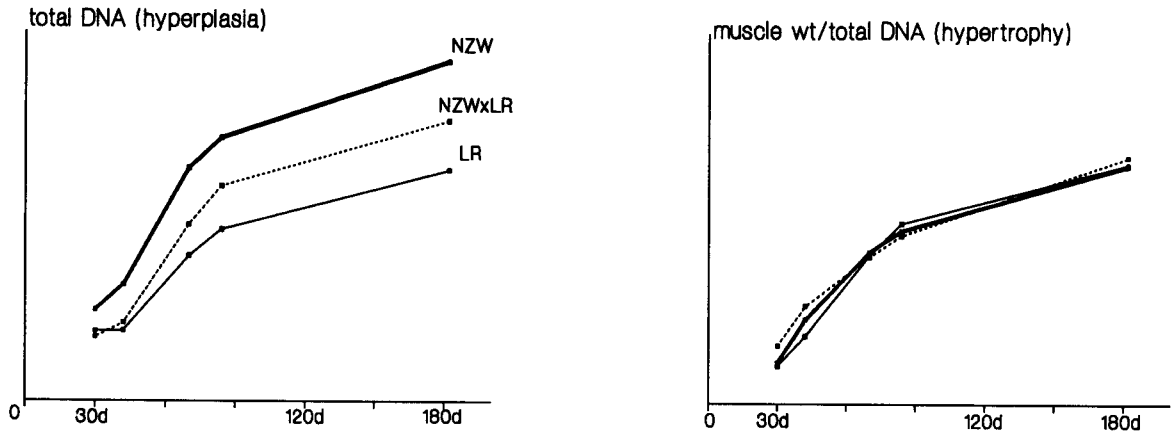
In the rabbit, muscle fibres continue to multiply after birth. This lasts longer (up to 17 days) in the muscles which relative growth is slow (NOUGUES, 1972). Muscle weight thereafter increases as a result of lengthening of the fibres, which follows bone growth, and of increasing in diameter which continues for much longer (figure 1).

Figure 1 : Lengthening and thickening of fibres in *accessorius latissimi dorsi* and *soleus* muscles of the rabbit during growth (after NOUGUES, 1973)



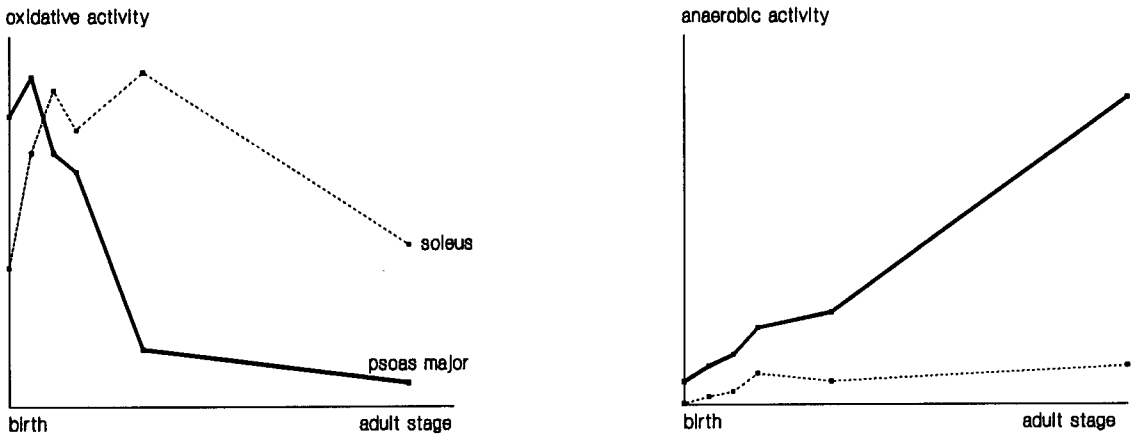
Cell multiplication carries on for a long time. Between 30 and 84 days after birth the amount of DNA, which is a good index for hyperplasia, is multiplied by 2.9 in hind leg muscles pooled together, whilst the ratio of muscle weight to DNA content, which estimates the mass of mononucleate cells, is only multiplied by 1.4 (OUHAYOUN and ROUVIER, 1973). Using these criteria, comparison of breeds differing in adult weight shows that the mitotic capacity of the satellite cells is the most relevant factor for explaining differences in muscle weight, and hence differences in global body weight increase too (figure 2).

Figure 2 : Hyperplasia and cellular hypertrophy in the whole musculature of hind leg in New Zealand White (NZ), (New Zealand White x Little Russian) and Little Russian (LR) rabbits between days 28 and 182 (after OUHAYOUN and ROUVIER, 1973)



In red muscles (which are oxidative in the adult) the oxidative enzyme activity increases after birth, reaches a maximum 30 days later and then decreases, whilst the glycolytic activity remains very low up to the adult stage. In white muscles (which are glycolytic in the adults) the glycolytic activity increases as the animal grows and this carries on beyond day 30, whilst the oxidative activity decreases after birth especially before day 30 (BACOU and VIGNERON, 1976) (figure 3).

Figure 3 : Evolution of the metabolic activity in *psoas major* (pure αW) and *soleus* (pure βR) muscles of common rabbits (after VIGNERON and BACOU, 1976a).



The ratios between the different nitrogen fractions [myofibrillar proteins (myosin, actin, troponin, tropomyosin), sarcoplasmic proteins (enzymes involved in glycolysis, creatine kinase, myoglobin), stroma proteins (collagen, reticulin, elastin) and non-protein nitrogen] change after birth at different rates according to the muscles, but always fast enough for a permanent equilibrium to be reached on the 11th day after birth (VIGNERON, 1973).

Muscle fibres thus gradually acquire the functional and metabolic properties which make them suitable for specific movements and postures: i.e. oxidative or glycolytic energy metabolism, slow or fast contraction, which enables either a moderate and prolonged or a short and intense muscular activity.

MUSCLE BIOCHEMISTRY AND MEAT QUALITY

The biochemical changes in muscle tissue after slaughtering slowly turn it into meat. First of all, during the onset of *rigor mortis*, hydrolytic reactions of the anaerobic pathway use up the energy reserves (ATP, creatine phosphate, glycogen): the muscle tissue becomes more acid (the pH can drop by as much as 1.5 units), the contractile protein system becomes unstretchable. The new organisation is accompanied by a decrease in the **water holding capacity** and by an increase of **brightness** of meat. Secondly, during the maturation phase, proteolytic reactions affect the ordering of the myofibril system and to a lesser extent that of collagen: the **tenderness** of the meat increases. The **flavour** of the meat, which is a combination of gustative and olfactive properties, develops. This mainly depends on how much lipids the meat contains and on their composition and chemical stability (lipolysis, possibly oxidation), but the flavour can also be enhanced by the products of the hydrolysis and deamination of ATP (inosine, hypoxanthine).

Red muscles are the best endowed with mitochondria, where oxidative phosphorylation takes place, with myoglobin, an oxygen carrying pigment, and with intracellular lipids, an energetic substrate. Red muscles are better irrigated and contain fibres with a smaller diameter than white muscles; they also have a higher phospholipid content. As a result their colour is richer, their flavour strong and their juiciness high. In the rabbit red muscles include most of the fore part of the carcass and the fusiform muscles of the inner part of the thigh (*semimembranosus proprius* muscle) and of the leg (*soleus* muscle). Tenderness is on the one hand linked to the amount and quality of collagen, and on the other to the amount of myofibrillar proteins and to what extent they have been denaturated by hydrolytic processes during maturation. Considering that rabbits are slaughtered when fairly young (10–11 weeks old) the reticulation of the collagen is not an issue as far as tenderness is concerned, not even in collagen-rich red muscles (after GILKA and HORNICH, 1975). However toughness can occur in rabbit meat, especially in white muscles where contractile proteins are particularly abundant (GILKA and HORNICH, 1975) despite their higher sensitivness to proteolysis during maturation (OUALI and VALIN, 1984). Moreover, the maturation parameters for rabbit meat are not ideal for tenderness.

According to DRANSFIELD *et al.* (1981), cited by OUALI and VALIN (1984) the maturation rate in rabbit is twice as slow as in pork and half as intense as in beef. However, if the carcasses are cooled rapidly, at least in the case where the meat temperature remains positive for the first three hours *post mortem*, then the intensity of cold shortening is weak and should have no impact on meat tenderness (OUHAYOUN *et al.*, 1990).

REPORT ON STUDIES RELATING TO THE ENERGY METABOLISM OF MUSCLES AND CORRELATED TRAITS

The work described here has been undertaken to answer a crucial question in meat production. Can the diversity of rabbit production conditions (slaughter age, feeding) and the genetic improvement of growth performance (selection between and within lines, and crossings) bring about variations in the energy metabolism of muscles and then in the meat quality? The impact of processing on meat quality (*peri mortem* conditions rabbits are submitted to), which has also been addressed, is not discussed here.

1. Physical and chemical parameters studied

Several parameters can be used to give some indication as to the state of the energy metabolism of muscles in a live animal or as to its evolution during the onset of *rigor mortis*. In the results reported here, energy metabolism was estimated by measuring the activity of enzymes used as indicators for the **glycolytic** pathway (fructose -1.6- diphosphate aldolase: EC 4.1.2.13) and for the **oxidative** pathway (isocitrate dehydrogenase: EC 1.1.1.41). Enzymes were extracted using the method described in Ansay (1974) and titrated by continuous kinetics, following the oxidation rate of NADH + H+ (aldolase) or the reduction rate of NADP+ (dehydrogenase). The myofibrillar, sarcoplasmic, stroma and non-protein nitrogen fractions, which are all modified during functional and metabolic differentiation, were separated by differential solubility using the method of Helander (1957). Haem pigments were extracted in a water/aceton/HCl solution according to HORNSEY's method (1956) and measured by spectrophotometry (512 nm). The pH of muscles was measured either *in situ* after incision of muscles indexed in a reproductible way, or after crushing muscle samples in 5 mM sodium iodoacetate so as to block the active –SH site of 3P–glyceraldehyde dehydrogenase and thus interrupt glycolysis.

The *post mortem* evolution of pH is noteworthy in that it affects the brightness of meat, its water holding capacity and hence its toughness too. Therefore it is important to understand the relationship between muscle acidification kinetics and biochemical characteristics of muscle. On the other hand, an unusual evolution of the muscule pH might be interpreted in terms of equilibrium variations in the energy metabolism of muscles.

2. Between-muscle variations

Acidification in red muscles is slower and not as thorough as in white muscles, despite the weak buffering capacity of the former (TALMANT *et al.*, 1986). These kinetics are due to their lower glycolytic capacity: they have less glycogen and a smaller amount of enzymes belonging to the anaerobic glycolytic pathway.

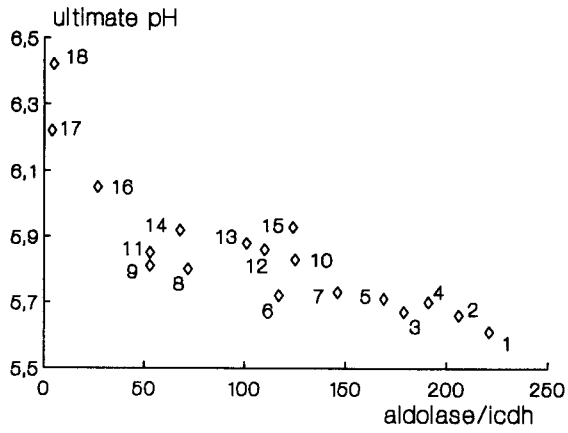
In the rabbit there is a higher myofibrillar, sarcoplasmic and non-protein nitrogen content in the *longissimus dorsi* muscle than in the *biceps femoris* muscle but the reverse holds for the stroma (connective tissue). This difference in composition accounts for the fact that the *longissimus dorsi* muscle is faster and more glycolytic (OUHAYOUN and DELMAS, 1983). Under a set of well–defined *peri mortem* conditions (fasting, transport, carcass chilling...) *post mortem* pH fall for 24 hours is more rapid in the *longissimus dorsi* muscle than in the *biceps femoris* muscle (OUHAYOUN and DELMAS, 1988) (time in mn):

longissimus dorsi : $pH = 6.52 \times e^{-0.000115\ t}$
biceps femoris : $pH = 6.39 \times e^{-0.000079\ t}$

Nevertheless, 30 mn after stunning and during the first hours of chilling, the pH drops faster in the *biceps femoris* muscle despite its relatively more oxidative metabolism. This could be due to the glycogenolytic effect of catecholamines released during stunning which are particularly active in well irrigated red muscles.

The pH drop has a weaker amplitude in red muscles than in white muscles. Within a single animal the ultimate pH (pHu) ranges between 5.4 and 6.4 according to the muscle location. The more glycolytic the muscle's energy metabolism (high aldolase/dehydrogenase ratio), the more acid the pH. Red muscles, which have a high pH, are mainly located in the fore part of the carcass (DELMAS and OUHAYOUN, 1990) (figure 4).

Figure 4 : Relationship between energy metabolism balance (aldolase/ICDH) and ultimate pH (pHu) in several muscles (after DELMAS and OUHAYOUN, 1990)



1: *longissimus dorsi* (post. part); **2**: *longissimus dorsi* (interm. part); **3**: *semimembranosus accessorius;* **4**: *psoas major;* **5**: *parameralis;* **6**: *adductor brevis et magnus;* **7**: *biceps femoris;* **8**: *gastrocnemius;* **9**: *teres major;* **10**: *tensor fasciae latae;* **11**: *triceps brachii;* **12**: *semitendinosus;* **13**: *longissimus dorsi* (ant. part); **14**: *biceps brachii;* **15**: *gracilis;* **16**: *supraspinatus;* **17**: *semimembranosus proprius;* **18**: *soleus.*

The variability of the energy metabolism and of the ultimate pH, as observed between different locations in the *longissimus dorsi* muscle, results from the heterogeneousness of the balance between fibres of different metabolic and contractile types (VIGNERON, BACOU and ASHMORE, 1976; DELMAS and OUHAYOUN, 1990). This is the reason why BLASCO, OUHAYOUN & MASOERO (1992) recommend that muscle pH measurements be carried out at a specific location, i.e. near the 5th lumbar vertebra.

Because acidification is slower and has a weaker amplitude in the *biceps femoris* muscle than in the *longissimus dorsi* muscle, the water holding capacity is greater (HAUBOLD, 1974).

Changes in the haem pigments concentration during development are most likely due to two contradictory facts: on the one hand a decrease occurs in the muscle's energy metabolism which becomes less and less oxidative, and on the other hand haem pigments accumulate with age. These antagonistic trends set up a balance depending on the muscle. Therefore the interpretation of the variability of the haem pigments content of muscles is quite a complex matter. However, it has been established that within a single animal the haem pigments content differs between muscles according to their fibre composition. For example the haem pigments content of 11-week old *New Zealand White* rabbits is 1.26 times as high in the *biceps femoris* muscle (72 mg myoglobin/100 g fresh muscle) as in the less oxidative *longissimus dorsi* muscle (57 mg/100 g) (OUHAYOUN, DELMAS and POUJARDIEU, 1982).

3. Variations during growth

3.1. Effect of weight

Meat rabbits are usually slaughtered when they have reached at least 50 % of the adult weight. This is done so as to optimize the production performance (growth rate and feed efficiency) and the commercial value (slaughter yield, muscle/bone ratio and fat content of the carcass). The age at which this stage is reached varies because of the high variability of the precocity of rabbit growth, but it usually lies between 70 and 77 days. ROIRON, OUHAYOUN and DELMAS (1992) have quantified the influence of age and weight at slaughter on commercial value. They compared rabbits that had reached 2.2, 2.4 or 2.6 kg in 70 or 77 days. The results indicate that whichever character is considered, the effect of age (and hence of precocity of growth) is negligible and the effect of weight is more important. Carcass heaviness increases the slaughter yield, the muscle/bone ratio and the fat content of the carcass noticeably. This evolution agrees with the allometric relations given by CANTIER et al. (1969) for tissues and organs. On the other hand, the ultimate pH of the musculature is lower in heavy rabbits. However, this acidification of the meat does not lead to any increase in the cooking loss. Therefore, it seems that the metabolic differentiation of muscle tissue, which manifests itself as the development of the glycolytic metabolism at the expense of the oxidative metabolism (BACOU and VIGNERON, 1976a), is both very long-lasting and important considering the variations in the ultimate pH in rabbits whose weights differ by as little as 0.2 to 0.4 kg. DALLE ZOTTE and OUHAYOUN (1993) have shown that the variations in the ultimate pH in muscles are indeed the result of continuing metabolic differentiation during fattening.

3.2. Effect of diet

Insofar as the protein content of the diet has very important consequences on the weight growth rate during fattening, quantifying its possible consequences on the biochemistry of muscles, especially on the balance between the protein fractions and on the energy metabolism was of some interest. OUHAYOUN and DELMAS (1983) have compared the production performance and biochemistry of muscles in 11–week old rabbits that had been fed *ad libitum* since weaning on diets differing in their protein/digestible energy ratio (43 < P/E < 71 g/1000 kcal). The growth rate

Table 2 : Influence of the protein/energy ratio (P/E: g/1000 kcal digestible energy) on the growth rate (ADG) between weeks 4 and 11 and on the characteristics of the *longissimus dorsi* and *biceps femoris* muscles (OUHAYOUN and DELMAS, 1983)

		longissimus dorsi				*biceps femoris*			
P/E	ADG (g/d)	% LW	% N	% N sarco.	aldolase (UI/g)	% LW	% N	% N sarco.	aldolase (UI/g)
71.1	43.3	2.82	3.76	24.4	854	0.58	3.77	21.9	686
57.0	41.4	2.81	3.70	24.3	803	0.56	3.68	21.9	661
43.0	34.5	2.45	3.54	22.8	711	0.55	3.56	20.2	582
P(1)	**	**	**	**	**	NS	**	**	**

(1) **: P < 0.01; NS: P > 0.05 ; % LW = weight of the muscle in % of the live weight ; % N Sarco. = Sarcoplasmic nitrogen as % of the total N.

increases with the P/E ratio of the feed and is accompanied by a better relative development of the musculature. The musculature itself has a higher nitrogen content. The sarcoplasmic protein content and the glycolytic enzyme activity increase (table 2). The correlation of their variations is due to the fact that 70 % of sarcoplasmic proteins are involved in the glycolytic process (Scopes, 1970). Two hypotheses could account for these effects on muscle biochemistry. The feed protein level could act directly on the global protein anabolism and on each of the protein fractions, as mentioned by ASHGAR and YEATES (1979) and ANTOSZEWSKA (1979) in sheep and chicken, respectively. The protein level could also act indirectly by modifying the weight at which rabbits are slaughtered, as described above (paragraph 4.3.1). The latter hypothesis agrees with the observation of ASHGAR *et al.* (1981) that restricted (lightweight) rabbits have a higher ultimate pH (and hence a less glycolytic energy metabolism) than (heavier) rabbits that underwent a compensating growth after *ad libitum* feeding was resumed.

3.3. Growth factors

Several hormones play a part in the development and growth of muscles. They act on cell proliferation (Fibroblast Growth Factor), on the fusion of myoblasts (PGE1 prostaglandins, insulin, IGF-growth factors secreted by the liver especially when stimulated by somatotropin), on protein synthesis (IGF and insulin) or on the transition of fibres from foetal to adult type (thyroid hormones) (ROBELIN, 1990).

In the growing pig, somatotropin reduces lipogenesis and enhances proteinogenesis. It also increases the growth rate and the feed efficiency. Its effects on muscle biology and on meat quality are being actively studied (BONNEAU, 1990). Recombinant porcine somatotropin (rpST), which has some physical and chemical similarities with rabbit somatotropin has been used as a model for studying rabbit growth (HULOT, OUHAYOUN and DALLE ZOTTE, 1992). These authors have given one daily intramuscular injection of rpST (100 μg) for 21 days to rabbits initially aged 70 days. Growth rate and feed efficiency were not affected by the treatment. Nevertheless, rpST reduced fatness and increased proteinogenesis. It also decreased the ultimate pH of muscles (table 3).

This decrease of the muscle pH might be due to a stimulation of the glycolytic potential by the heterologous hormone, possibly via a modification of the equilibrium of the energy metabolism. This aspect is under intense scrutiny.

4. Genetic variations

The literature does not report any abnormal *post mortem* acidification kinetics characteristic of DFD (dark, firm and dry, high pH), PSE (pale, soft and exsudative, with a fast acidification) or acidic meat (low ultimate pH) in Rabbit. This also holds when the animals are stunned by electric shock (270 V) (CIVERA et al., 1989, OUHAYOUN, DAUDIN and RAYNAL, 1990). It has been established that this method, compared to the breaking of the spinal chord, accelerates the depletion of glycogen, ATP and P-creatin reserves and hence also accelerates the acidification of muscles (OUHAYOUN and POUJARDIEU, 1990). However, several research results mention genetic variations of the pH of muscles.

Table 3. Main effects of recombinant porcine somatotropin on the rabbit (HULOT, OUHAYOUN and DALLE ZOTTE, 1992)

	Treatment		P(1)
	rpST	control	
Growth rate (70–90 d)(g/d)	25.2	25.5	NS
Feed consumption (70–90 d)(g/d)	149.4	156.3	NS
Slaughter yield (%)	60.2	60.1	NS
Skin weight (%)	14.3	13.4	**
Protein content (2) (% of ref carc)	20.5	19.9	*
Lipid content (%)	9.4	10.8	*
Perirenal fat weight (%)	2.01	2.72	***
P/M+S FA ratio (3)	0.32	0.28	
pHu(4) *semimembranosus accessorius*	5.67	5.78	**
biceps femoris	5.65	5.74	*
tensor fasciae latae	5.80	5.78	NS

(1) NS P > 0.05; * P < 0.10; ** P < 0.05, *** P < 0.01

(2) reference carcass weight according to Blasco, Ouhayoun and Masoero (1992)

(3) polyunsaturated to (monunsaturated + saturated) fatty acids ratio

(4) ultimate pH (24 h post mortem)

Table 4 : Between breed variations of the fibre composition of rabbit muscles (after BACOU and VIGNERON, 1976B)

Breeds	βR	αR	αW
Garennes (wild rabbits)	7.8 bc	19.4 a	72.9 a
Little Russian	6.2 a	16.5 b	77.4 b
New Zealand White	8.7 cd	14.8 c	76.4 b
Flemish Giant	6.9 ab	14.1 c	79.0 c

mean values with different letters in a vertical row are significantly different ($P < 0.05$)

4.1. Variations between breeds, lines and crossings

According to NATH and RAO (1985), the ultimate pH (pHu) of meat is higher in the wild rabbit (*Oryctolagus hispidus*) than in the tame rabbit (*Oryctolagus cuniculus*) and correlatively it also has a higher water holding capacity ($r_{pHu,\ WHC} = 0.82$). In the domestic rabbit, the pHu varies from one breed to another (KUZNIEWICZ and WOJSYK-KUZNIEWICZ, 1976; BLASCO and PILES, 1990; PERRIER and OUHAYOUN, 1990; KROGMEIER and DZAPO, 1991), however the differences observed are generally small (a few hundredths of a pH unit). These variations can be attributed to differences in muscle composition. For instance, the muscles of the Flemish Giant rabbit contain more αW fibres -at the expense of αR fibres- than those of the wild rabbit or those of the New Zealand White or Little Russian breeds (BACOU and VIGNERON, 1976b) (table 4).

This characteristic of the Flemish Giant breed is also observed in crossings (OUHAYOUN, 1978) (table 5).

Table 5 : Variations between rabbits obtained by crossing INRA 1067 females with males of different genetic types of the energy metabolism balance (aldolase/ICDH) in hind leg muscles (OUHAYOUN, 1978)

Breeds or crosses	aldolase / ICDH
Coloured dwarf	97
New Zealand White	103
Rex	104
Dutch x Little Russian	111
Flemish Giant	122

The haem pigments content varies little between breeds: in the *transversus abdominis* muscle of 856 eleven-week old crossed rabbits obtained from four "male" lines used in terminal crossings for obtaining medium-sized rabbits, it ranged from 103 to 118 mg/100 g, according to the line (OUHAYOUN, DELMAS and POUJARDIEU, 1982).

The variations of metabolic equilibrium between breeds result in some cases from differences in precocity. This has been shown in a comparative study between the Little Russian and New Zealand White breeds (OUHAYOUN, DELMAS and POUJARDIEU, 1982). As expected, between days 30 and 103, the weight increase of the *longissimus dorsi* and *biceps femoris* muscles was correlated with a significant increase in glycolytic activity and with a significant decrease in activity of oxidative enzymes, the evolution of the energy metabolism being significantly more marked in the *biceps femoris* muscle. However, the pattern of oxidative metabolism showed marked differences between both breeds: the decrease in oxidative (ICDH) activity was significantly faster in Little Russian than in New Zealand White rabbits (table 6). Thus, the early maturity of the Little Russian breed, already evidenced in terms of body composition (OUHAYOUN, 1980) was confirmed by the variations in the late muscular metabolic differentiation.

4.2. Within-breed variability

The genetic relationship between growth characters and the metabolism of muscle tissue has been studied in over 1600 rabbits (70 sires and 239 dams) at the Progeny Testing Station, Toulouse (OUHAYOUN, ROUVIER and POUJARDIEU, 1974). An estimate of within class and between classes correlations was obtained using sire variance and covariance components. The following conclusions were drawn in this study:

1 – no differences were found between male and female rabbits for body weight at 4, 10 and 11 weeks, average daily gain between 4 and 10 weeks, carcass weight and pH of the *biceps femoris* muscle at 30 mn and 24 h *post mortem* ;
2 – genetic variability of muscle pH was quite high at both times (table 7a) ;
3 – the genetic correlations between muscle ultimate pH and growth characters were moderately high and negative (table 7b).

Table 6 : Energy metabolism changes in muscles during growth. Comparison of the relationship between enzyme activities (UI/g) (dependent variables) and weight (g) of muscles (independent variable) in New Zealand White and Little Russian rabbits (after OUHAYOUN, DELMAS and POUJARDIEU, 1982)

		ICDH	aldolase
New Zealand White	b	−0.0697	0.0216
	s_b	0.0069	0.0034
	r(2)	−0.91**	0.81**
Little Russian		−0.1133	0.0182
	s_b	0.0127	0.0057
	r(2)	−0.89**	0.57**
t(1)		*3.12***	*0.53 NS*
Longissimus dorsi	b	−0.0775	0.0275
	s_b	0.0089	0.0043
	r(2)	−0.82**	0.72**
Biceps femoris	b	−0.2767	0.1149
	s_b	0.0421	0.0215
	r(2)	−0.73**	0.65*
t(1)		*4.43***	*3.68***

*(1) comparison of regression coefficients (b): NS parallel slopes, ** non parallel slopes (P < 0.01)*
*(2) significance of correlation coefficients: NS non significant (P > 0.05); ** highly significant (P < 0.01)*

Table 7a : Within class (sire) correlations of growth and slaughter criteria (OUHAYOUN, ROUVIER and POUJARDIEU, 1974)

	males	females	both sex
Weight at 4 weeks	0.07	0.11	0.09
Weight at 10 weeks	0.18	0.19	0.18
Average daily gain (4–10 weeks)	0.17	0.16	0.15
Weight at 11 weeks	0.10	0.17	0.14
Weight of hot carcass	0.12	0.19	0.15
pH 30 mn of *biceps femoris* muscle	0.10	0.10	0.12
pH 24 h of *biceps femoris* muscle	0.19	0.19	0.18

Table 7b : Between class (sire) correlations between growth criteria and muscle pH at 30 mn and 24 h *post mortem* (OUHAYOUN, ROUVIER and POUJARDIEU, 1974)

	males		females		both sex	
	30mn	24 h	30mn	24 h	30mn	24 h
Weight at 4 weeks	0.05	−0.23	0.01	−0.16	−0.02	−0.34
Weight at 10 weeks	0.14	−0.46	0.16	−0.50	0.16	−0.48
Average daily gain (4–10 weeks)	0.20	−0.58	0.21	−0.63	0.25	−0.55
Weight at 11 weeks	0.28	−0.60	0.19	−0.55	0.22	−0.55
Weight of hot carcass	0.19	−0.63	0.14	−0.53	0.16	−0.56

Elsewhere, OUHAYOUN, DELMAS and POUJARDIEU (1982) have pointed out that within sire class correlation coefficients for haem pigments concentrations are moderate (0.05 to 0.13 depending on the estimation). The genetic correlations between muscle haem pigments content and growth characters are negative (–0.09 to –0.25 depending on the estimation). Thus, there is a slight antagonism between growth performance and muscle haem pigments content.

All these results indicate that selecting for fast growth rates might also favour a glycolytic energy metabolism in muscle tissue and in theory might spoil meat quality: tenderness by reducing the water holding capacity, flavour and juiciness by lack of intracellular lipids.

CONCLUSION

The muscle tissue is a composite tissue whose characteristics evolve during growth. In the rabbit, the multiplication of fibres and the synthesis of DNA, which translate the potential for muscle growth, carry on for a few weeks and several months after birth, respectively. Differentiation, especially metabolic differentiation, continues well after birth and leads to muscles which, when mature (this stage is only reached after the age at which rabbits are slaughtered for their meat) display a variety of contractile and metabolic properties. As a result, the criteria which account for the *post mortem* evolution of muscles, and the quality of meats obtained, vary widely between muscles. The rate and amplitude of muscle differentiation, which are specific to each breed and/or family, are responsible for the genetic variability of muscle composition (distribution of fibres into different types, balance between the enzymatic activities specific to each major pathway, proportion of the different protein fractions, haem pigments content) and of the criteria that account for *post mortem* evolution (acidification kinetics). This variability should be taken account of in programmes for the genetic improvement of growth, both when choosing breeds and when selecting within a breed. The lasting character of muscle differentiation in the rabbit probably explains the sensitivity of the metabolic parameters to certain biological factors (somatotropin) or production conditions (dietary nutrient balance, slaughter weight), even when these are applied quite late. These results all show that further research into muscle differentiation might lead to the prediction or even the avoidance of meat quality deficiencies in the rabbit.

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BIBLIOGRAPHY

ANSAY M., 1974. Développement biochimique du muscle de foetus bovin. 3- Enzymes et différenciation. *Ann. Biol. anim. Bioch. Biophys., 14, 105-116*

ANTOSZEWSKA B., 1979. Effect of feeding level on the content of basic protein fractions in the pectoral and leg muscles of growing white Plymouth rock hens. *Pr. Mater. Zootech., 18, 77-91*

ASGHAR A, PEARSON A.M., MAGEE W.T., TAHIR M.A., 1981. Effects of *ad libitum*, maintenance and sub-maintenance feeding and of compensatory growth on some biochemical properties of muscle from weanling rabbits. *Journal of Nutrition, 111, 1343-1352*

ASGHAR A., YEATES N.T.M., 1979. Muscle characteristics and meat quality of lambs grown on different nutritional planes. 2- Chemical and biochemical effects on muscle. *Agric. Biol. Chem., 43, 437-444*

ASHMORE C.R., DOERR L., 1971. Postnatal development of fiber types in normal and dystrophic skeletal muscle of the chick. *Exp. Neurol., 30, 441-446*

BACOU F., 1972. Evolution quantitative de l'aldolase, de l'aspartate aminotransférase, de la succinodéshydrogènase et de l'acétylcholinestérase dans les muscles blancs du lapin au cours de la croissance postnatale. *C.R. Soc. Biol., Montpellier, 1037-1042*

BACOU F., VIGNERON P., 1976a. Evolution périnatale des voies métaboliques glycolytique et oxydative de divers types de muscles squelettiques du lapin et du poulet. *Ann. Biol. anim. Bioch. Biophys., 16, 675-686*

BACOU F., VIGNERON P., 1976b. Métabolisme de divers types de muscles chez trois races de lapin de format différent. *Ist World Rabbit Congress, Dijon*

BACOU F., VIGNERON P., 1988. Propriétés des fibres musculaires squelettiques. 1- Influence de l'innervation motrice . *Reprod. Nutr. Dévelop., 28, 1387-1453*

BLASCO A., OUHAYOUN J., MASOERO G., 1992. Study of rabbit meat and carcass: criteria and terminology. *Options Méditerranéennes, Série Séminaires, 17, 105-120*

BLASCO A., PILES M., 1990. Muscular pH of rabbit. *Ann. Zootech., 39, 133-136*

BONNEAU M., 1990. Régulation de la croissance du porc par la somatotropine et les autres hormones de l'axe somatotrope: sécrétion, mécanismes d'action et effets sur les performances. *J. Rech. porcine en France, 22, 51-68*

CANTIER J., VÉZINHET A., ROUVIER R., DAUZIER L., 1969. Allométrie de croissance chez le lapin (Oryctolagus cuniculus). 1- Principaux organes

et tissus. *Ann. Biol. anim. Bioch. Biophys., 9, 5-39*

CIVERA T., JULINI M., QUAGLINO G., FERRERO E., 1989. Influence of stunning methods on quality of rabbit meat. *Industrie Alimentari, 28, 492-495*

DALLE ZOTTE A., 1992. Studio del metabolismo energetico muscolare in varie specie di interesse zootecnico.. *Corso de Dottorato de Ricerca in "Scienze Zootecniche", Università Degli Studi di Firenze, Padova e Udine*

DALLE ZOTTE A., OUHAYOUN J., 1993. Postweaning evolution of muscular energy metabolism and related physico-chemical traits in rabbit. *5th Hungarian Rabbit Science Symposium, Kaposvar*

DELMAS D., OUHAYOUN J., 1990. Technologie de l'abattage du lapin. 1- Etude descriptive de la musculature. *V. P. C., 11, 11-14*

GILKA J., HORNICH M., 1975. The colour of some rabbit muscles and the content of connective tissue. *Zivocisna Vyroba, 20, 763-772*

HAUBOLD W., 1974. Investigations on carcass and meat quality of broiler rabbits of different breeds and their crosses. 2- Meat quality of broiler rabbits. *Monatshefte für Veterinärmedizin, 29, 348-351*

HELANDER E., 1957. On quantitative muscle protein determination. *Acta physiol. Scand., suppl., 141, 9-95*

HORNSEY H.C., 1956. The colour of cooked cured pork. 1- Estimation of the nitric oxide-haem pigments. *J. Sci. Food Agric., 7, 534-540*

HULOT F., OUHAYOUN J., DALLE ZOTTE A., 1992. Rabbit growth, feed efficiency and body composition. Effects of recombinant porcine somatotropin. *Vth World Rabbit Congress, Corvallis*

KROGMEIER D, DZAPO V., 1991. Performance traits of rabbits of the New Zealand White and Helle Grosssilber breeds and their reciprocal crosses. 2- Heterosis effects on growth intensity, carcass traits ande meat quality traits. *Archiv für Geflügelkunde, 55, 162-169*

KUZNIEWICZ J., WOJSYK-KUZNIEWICZ A., 1976. Slaughter value of broiler rabbits. *Przemysl Spozywczy, 32, 303-305*

LEFAUCHEUR L., 1989. Les différents types de fibres musculaires chez le Porc. *INRA Prod. Anim., 2, 205-213*

NATH D.R., RAO P.L.N., 1985. A comparison between domestic and wild rabbits as meat and fur producers. *Indian J. Anim. Prod. and Manag., 1, 136-140*

NOUGUES J., 1972. C.R. Etude de l'évolution du nombre des fibres musculaires au cours de la croissance postnatale du muscle chez le lapin. *Soc. Biol. Montpellier, 166, 165-172*

NOUGUES J., 1973. Etude histologique de la croissance postnatale des muscles *Soleus* et *Accessorius latissimi dorsi* chez le lapin commun. *Ann. Biol. anim. Bioch. Biophys., 13, 37-50*

OUALI A., VALIN C., 1984. Principaux facteurs technologiques et biologiques influant sur le processus de maturation des viandes. *Bull. Tech. CRVZ Theix, 55, 73-78*

OUHAYOUN J., 1978. Etude comparative de races de lapins différant par le poids adulte. Incidence du format paternel sur les composantes de la croissance des lapereaux issus de croisement terminal. *Thèse, Montpellier*

OUHAYOUN J., 1980. Evolution comparée de la composition corporelle de lapins de trois types génétiques au cours du développement postnatal. *Reprod. Nutr. Dévelop., 20, 949-959*

OUHAYOUN J., DALLE ZOTTE A., 1993. Muscular energy metabolism and related traits in rabbit. *Vth Hungarian Rabbit Science Symposium, Kaposvar*

OUHAYOUN J., DAUDIN J.D., RAYNAL H., 1990. Technology of rabbit slaughter. 2- Effects of temperature of the chilling air on moisture loss and acidification of the muscle tissue. *Viandes et Produits carnés, 11, 69-73*

OUHAYOUN J., DELMAS D., 1983. Valorisation comparée d'aliments à niveaux protéiques différents, par des lapins sélectionnés sur la vitesse de croissance et par des lapins provenant d'élevages traditionnels. 2- Etude de la composition azotée et du métabolisme énergétique des muscles *L. dorsi* et *B. femoris. Ann. Zootech., 32, 277-286*

OUHAYOUN J., DELMAS D., 1988. Meat quality of rabbit. 1- Differences between muscles in *post mortem* pH. *4th World Rabbit Congress, Budapest*

OUHAYOUN J., DELMAS D., MONIN G., ROUBISCOUL P., 1990. Abattage du lapin. 2- Effet du mode de réfrigération sur la biochimie et la contraction des muscles. *5èmes J. Rech. cunic., Paris*

OUHAYOUN J., DELMAS D., POUJARDIEU B., 1982. Variability in the myoglobin content of rabbit muscle. Relationships with energy metabolism. *II. Internationales Kolloquium "Das Kaninchen als Modeltier und Züchtungsobjekt", Rostock*

OUHAYOUN J., POUJARDIEU B., 1990. Abattage du lapin. 1- Effet des modes d'étourdissement et de réfrigération sur l'évolution de la longueur des sarcomères. *5èmes J. Rech. cunic., Paris*

OUHAYOUN J., ROUVIER R., 1973. Rôles de la multiplication nucléaire et du grandissement cellulaire dans la croissance musculaire de lapins de plusieurs génotypes. *J. Rech. avic. cunic., Paris*

OUHAYOUN J., ROUVIER R., POUJARDIEU B., 1974. Relations génétiques entre les performances de croissance pondérale et le métabolisme du tissu musculaire du lapin. *Ist World Congress on Genetics applied to Livestock Production, Madrid*

PERRIER G., OUHAYOUN J., 1990. Diversification des carcasses. Croissance et qualités bouchères de lapins issus du croisement de mâles Argenté de Champagne et de femelles hybrides. *5èmes J. Rech. cunic., Paris*

RANVIER M.L., 1873. Propriétés et structures différentes des muscles rouges et des muscles blancs chez le lapins et chez les raies. *C.R. Acad. Sci. Paris, 77, 1030-1035*

ROBELIN J., 1990. Différenciation, croissance et développement cellulaire du tissu musculaire. *INRA Prod. Anim., 3, 253-263*

ROIRON A., OUHAYOUN J., DELMAS D., 1992. Effets du poids et del'âge d'abattage sur les carcasses et la viande de lapin. *Cuniculture, 19, 143-146*

SCOPES L.K., 1970. Characterisation and study of sarcoplasmic proteins. *In : The Physiology and Biochemistry of Muscle as a Food, vol. II, Univ. Wisc. Press, 471-492*

TALMANT A., MONIN G., BRIAND M., DADET M., BRIAND Y., 1986. Activities of metabolic and contractile enzymes in 18 bovine muscles. *Meat Sci., 18, 23-40*

VIGNERON P., 1973. Evolution de la composition azotée des muscles *Psoas major* et *Longissimus dorsi*, de la naissance à 3 semaines chez le lapin. *Ann. Biol. anim. Bioch. Biophys., 13, 553-563*

VIGNERON P., BACOU F., ASHMORE C.R., 1976. Distribution heterogeneity of muscle fiber types in the rabbit *longissimus* muscle *J. Anim. Sci., 43, 985-988*