

The Effect of the RN⁻ Allele on Meat Quality and How the Gene was Discovered

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Introduction

The RN⁻ allele was first identified in France, and discovered as a negative effect on the yield of cured cooked hams in composite lines containing the Hampshire breed (Naveau, 1986; Le Roy et al., 1990). The name comes from Rendement Napole, where 'rendement' is the French word for yield, and Napole comes from the initial letters from the surnames of the inventors N. Naveau, P. Pommeret and P. Lechaux (Naveau et al., 1985). The dominant allele decreasing the yield was called RN⁻, resulting in so-called 'acid meat' due to the low ultimate pH, and the normal gene rn⁺. Thus three genotypes exist, RN⁻RN⁻, RN⁻rn⁺ and rn⁺rn⁺ (Naveau, 1986). Yield was assessed as 'Napole yield', a standardized laboratory method for estimating yield of cured and cooked ham (Naveau et al., 1985). In short, 100 g of *M. semimembranosus* was cut into 1 cm cubes, cured in 20 g of brine during 24 hours, and then cooked in a boiling water-bath for 10 minutes. The negative effect on Napole yield in carriers of the allele is substantial and was estimated to be as high as 8 percentage units (Fernandez et al., 1990).

Most research carried out on the effects of the RN⁻ allele has been done on animals either classified as carriers or non-carriers of the RN⁻ allele. In Sweden for example, a common commercial cross is the use of Hampshire sires on Landrace x Large White cross bred sows, making slaughter pigs either heterozygous RN⁻/rn⁺ or homozygous rn⁺/rn⁺. However, in a recent French study all three genotypes were studied, thus making it possible to differentiate between pigs being homozygous or heterozygous for the RN⁻ allele (Lebret et al., 1999; Le Roy et al., 2000a).

This paper summarises the main effects of the RN⁻ allele and how the gene was discovered including:

- Chemical composition and technological quality
- Enzyme activities and muscle fibre characteristics

- Processing quality
- Sensory quality
- Production characteristics
- Detection of the gene using differences in chemical composition
- Detection of the RN⁻ mutation and physiological effects of the gene

Chemical Composition and Technological Quality

Muscle from Hampshire pigs are known to have a higher glycogen content than other breeds, and Sayre et al. (1963) showed that Hampshire pigs had the same amount of glycogen at the end of the post-mortal glycolysis as muscles from other breeds at slaughter. The effect of the RN⁻ allele was early postulated to be due to an increase in the glycogen content of white muscles (Fernandez et al., 1990). This was usually measured as concentration of glycolytic potential (GP), i.e. the concentration of glycogen, glucose, glucose-6-phosphate and lactate (Monin and Sellier, 1985). The glycolytic potential is increased by approximately 70% in e.g. the white *longissimus* muscle in RN⁻ carriers (Fernandez et al., 1990; Estrade et al., 1993). In the study by Le Roy et al. (2000a) with all three RN genotypes, it was shown that the RN⁻ allele for muscle GP was completely dominant for the muscles *semimembranosus* and *semispinalis capitis* and almost completely dominant for the *longissimus* muscle.

When RN⁻ carriers were compared with non-carriers the protein content was 1 – 1.5 percentage units lower, while the water and ash content was the same or slightly higher (Monin et al., 1992; Estrade et al., 1993; Enfält et al., 1997a; Lundström et al., 1998b; Gariépy et al., 1999; Lebret et al., 1999). On the other hand, no effect was found on the total intra-muscular fat content (Monin et al., 1992; Lundström et al., 1998b; Lebret et al., 1999), while a higher proportion of omega-3 and C22:5 fatty acids was found in carriers of the RN⁻ allele (Nilzén et al., 2001). The hydroxyproline content was not affected by RN genotype (Lebret et al., 1999).

The change in chemical composition has of course an effect on the technological quality. The increase in glycogen content leads to a decrease in the ultimate pH, but usually with no effect on the rate of the pH decrease post mortem (Lebret et al., 1999). The lower ultimate pH is probably the

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main cause for the decrease in water-holding capacity both in the raw meat and during cooking (Lundström et al., 1996, 1998a,b; Enfält et al., 1997a,b; Le Roy et al., 2000), even if the lowered protein content is also of importance. The reflectance value, both measured as surface reflectance or internal reflectance, is usually higher in *RN* carriers indicating a paler meat (Lundström et al., 1996; Enfält et al., 1997a,b; Gariépy et al., 1999; Lebret et al., 1999), with slightly higher a^* and b^* values, i.e. more red and yellow meat in *RN* carriers (Le Roy et al., 2000a). No difference was found between heterozygous and homozygous carriers of the *RN* allele for ultimate pH and lightness, while the heterozygous genotype had higher a^* and b^* values, thus indicating an overdominance (Le Roy et al., 2000a). The protein solubility was shown to be slightly lower in *RN* carriers (Lundström et al., 1996; Gariépy et al., 1999), indicating a higher degree of protein denaturation, which might also contribute to the paler meat.

Enzyme Activities and Muscle Fibre Characteristics

In a comparison between Hampshire pigs and Yorkshire pigs, it was shown that muscles from Hampshire pigs were more oxidative (Essén-Gustavsson and Fjelkner-Modig, 1985). In the recent study by Lebret et al. (1999), the authors found that the white *longissimus* muscle was more oxidative in *RN* / *RN* pigs than in *rn*⁺ / *rn*⁺ pigs (higher activities of citrate synthase, CS, and b-hydroxy-acyl-coenzyme A dehydrogenase, HAD, and lower activity of lactate dehydrogenase, LDH). No significant difference was found between heterozygous and homozygous carriers of the *RN* allele, except for CS activity being higher in the homozygous pigs. In contrast, no effect of the *RN* allele was found on enzyme activities in the *semispinalis capitis* muscle.

As reviewed by Lebret et al. (1999), results for muscle fibre characteristics are somewhat contradictory when Hampshire pigs are compared with other breeds or the *RN* genotypes are compared. The authors found an increase in the relative areas of oxidative IIA fibres and a decrease in glycolytic IIBw fibres with an additive to an incompletely dominant effect of the *RN* allele. Using a slightly different mode of differentiation between fibre types, Lundström et al. (1998a) found similar results with a higher percentage of Type IIA and a lower percentage of IIB in *RN* carriers in comparison with non-carriers. A higher percentage of intermediate and a lower percentage of white fibres were also found when Hampshire pigs were compared with Landrace x Large White pigs (Feddern et al., 1995). Ruusunen & Poulanne (1997) detected a higher percentage of Type I and a lower percentage of IIB fibres together with higher capillary density in Hampshire pigs in comparison with Landrace or Yorkshire pigs. The results from the fibre studies are thus consistent with the enzymatic studies showing that *RN* carriers are more oxidative.

Processing Quality

Differences in processing yield between *RN* genotypes are highly dependent on the method of processing and the even-

tual use of additives such as phosphates. Without the addition of phosphates and using no tumbling, Lundström et al. (1998b) reported a difference of 4 percentage units (80.8 vs. 84.9% yield) between carriers and non-carriers of the *RN* allele after processing *M. semimembranosus et adductor* into cured cooked ham. No significant effect of the gene was found on curing yield, i.e. uptake of brine before cooking. Heyer (2000) found similar results, after commercial processing (but without tumbling) of the same muscle into cured smoked ham. Tumbling of loin muscles after injection of the brine resulted in a decreased difference between genotypes, with 2.2 percentage units higher yield in non-carriers (Lundström et al., 1998a). This difference between *RN* phenotypes is in accordance with other reports on ham processed without adding phosphates but with tumbling (Le Roy et al., 2000a).

One important question is if it is possible to avoid the negative effect of the *RN* allele on processing yield with the use of e.g. phosphates. The results are so far somewhat contradictory. Eber & Müller (1997) reported a highly significant difference in processing yield of 4.8 percentage units (94.2 vs. 99.0%) between carriers and non-carriers of the *RN* allele when the brine was without phosphates. With phosphates the difference disappeared (110.0 vs. 111.0%). On the other hand, Gariépy et al. (1999) found a significantly lower yield in *RN* carriers also after using brine containing the most common meat processing ingredients including phosphates (113.5 vs. 121.0%). Their conclusion was that meat from *RN* pigs can be used for cured products, but quality and yield will remain inferior in comparison with pork of normal quality.

Slicing ability is another important problem regarding processed meat from *RN* carriers. An early finding was that sliced ham from a composite line including Hampshire gave much higher slicing losses in comparison with hams from Pietrain or Large White x Pietrain (Chevillon et al., 1994). The defects could be described as separation of muscles in the slice, hole in the slice and areas with a crumbly structure. Electron microscopy revealed more alterations of the myofibrillar structure in cured-cooked *semimembranosus* muscle, with more disruptions at the level of Z-lines and more degraded thin filaments (Monin, 1995). Also with addition of polyphosphates in the brine the problem with low slicing ability remains. Gariépy et al. (1999) reported a slicing yield of 57% in carriers of the *RN* allele compared with 73% in non-carriers. The slicing yield was in this case expressed as percent weight of faultless slices to weight of the processed ham. The defective slices were incomplete or with holes or with separation problems.

The combined effects of the *RN* and the *HAL* genes on processed ham quality have been reported by Le Roy et al. (2000b). The interaction effect between the *RN* and *n* allele was significant, and in the genotype *RN*-*RN* *nn* a higher proportion was rejected for exudative status. However, in this genotype the unfavorable effect of *RN* on slice cohesiveness was reduced.

Sensory Quality

In several Swedish studies, the eating quality was enhanced in carriers of the *RN* allele. Pork from animals carrying the gene had higher juiciness, meat taste and acidulous taste and usually a higher tenderness when assessing the meat with a trained sensory panel (Johansson et al., 1999; Jonsäll et al., 2000a,b; Jonsäll et al., 2001). Also Swedish consumers preferred pork from carriers of the *RN* allele in comparison with non-carriers (Jonsäll et al., 2001). Cured-smoked loins from *RN* carriers also showed a higher initial and ultimate juiciness, less inhomogeneous appearance and lower hardness in sensory tests with a trained panel (Johansson et al., 1998), while cured-smoked ham (*M. biceps femoris*) from *RN* carriers were juicier and more acid (Josell et al., 1999). In a recent study (Heyer, 2000), where cured smoked *M. semimembranosus et adductor* was sensory tested, *RN* carriers had significantly higher tenderness, juiciness, smoked flavor, acidity, and salinity and lower bite resistance in comparison with non-carriers.

It is, however, still not quite clear which genotype the consumers prefer with regard to processed pork. In one study, consumers preferred processed ham from non-carriers (Lundström et al., 1998b), while those in the study by Heyer (2000) could not identify any difference between carriers and non-carriers, in spite of the profound positive effect of the *RN* allele when the test was performed with a trained panel.

In contrast to the generally very positive Swedish results concerning the *RN* allele on sensory quality, French results showed a negative effect of the *RN* allele on eating quality with lower tenderness and mellowness but higher pork flavor intensity (Le Roy et al., 2000a). The explanation of the differences between Sweden and France regarding the effect of the *RN* allele on eating quality can depend on differences in expression of the gene, but also on differences in aging and cooking procedures. In Sweden, the sensory tests are usually performed on pork after four days aging time, and using a relatively low cooking temperature at approximately 70°C. The sensory test in France was conducted after only 24 h aging time (Le Roy et al., 2000a) and at a cooking temperature at approximately 80°C (G. Monin, pers. comm.).

Production Characteristics

One main reason for the high gene frequency of the *RN* allele, which has been reported in e.g. Sweden (Enfält et al., 1997b; Josell et al., 2000), is an advantage in production characteristics for carriers of the *RN* allele. Carriers had higher daily gain, fewer days on test and produced carcasses with higher lean meat content and a larger proportion of ham. The major ham muscles were larger in the carriers and the proportion of glycolytic ham muscles was higher (Enfält et al., 1997a). Le Roy et al. (2000) compared all three genotypes and found a higher daily gain in heterozygous *RN* carriers than in non-carriers, while no difference was found between homozygous *RN* carriers and non-carriers. Heterozygous animals are thus the most favorable genotype concerning daily gain indicating overdominance. Also in the French study, the *RN* allele was

associated with leaner carcasses. Back fat thickness was decreased by about 1 S.D. in homozygous *RN* animals, with the heterozygotes being intermediate between the two homozygotes. In a French selection experiment, where the goal was to decrease the muscular glycolytic potential, an indirect unfavorable response on back fat thickness was found, but only a limited response on daily gain (Larzul et al., 1995). In contrast, Polish results indicated a higher response of the *RN* allele on daily gain than on back fat thickness (Kocwin-Podsiadla et al., 2000).

Detection of the Gene Using Differences in Chemical Composition

Before the DNA marker was finally established (Milan et al., 2000), the differences in chemical composition between *RN* phenotypes were used to identify carriers and non-carriers. Depending on which variable was used, a more or less pronounced bimodal distribution was obtained, and the valley between the peaks could be used as a threshold between phenotypes, i.e. carriers or non-carriers of the *RN* allele. The first trait used was the 'Napole yield', as a bimodal distribution was found, followed by GP (Fernandez et al., 1990). In GP lactate was included, but in our studies we obtained an accurate division between phenotypes using the concentration of glycogen, glucose, glucose-6-phosphate also without lactate (Lundström et al., 1996).

To facilitate finding of carcasses that were carriers of the *RN* allele, a quicker method was developed using only the concentration of glucose or the sum of [glucose] and [glucose-6-phosphate] in meat juice (Lundström and Enfält, 1997). Using [glucose] + [glucose-6-phosphate], 2% of the samples were misclassified in comparison with using GP, while [glucose] gave 7.5% misclassified samples. Glucose can be determined already at cutting in the slaughterhouse using the small portable instruments developed for blood glucose measurements, after centrifugation of the sample to obtain meat juice. Even if the test is not that accurate it can be used as a preliminary tool to obtain a more even distribution between samples from carriers and non-carriers of the *RN* allele, if the frequencies of the gene are as unequal as in Sweden. This test can then be verified in the laboratory by analysis of [glucose] + [glucose-6-phosphate] in meat juice, and finally by analysis of [glycogen] + [glucose] + [glucose-6-phosphate] in the meat. After the recent identification of the *RN* mutation, the last analysis will most likely be substituted by DNA-typing. In a commercial material, where a larger variation between animals can be expected, Heyer (2000) reported 4.6% misclassified animals. This classification into phenotypes was made using [glucose] and [glucose-6-phosphate] in meat juice, which was later compared with genotyping using the PCR method as described by Milan et al. (2000).

Another approach to determine the *RN* phenotype was developed by Josell et al. (2000), who used visual and near-infrared spectroscopy (NIR) through a fiber-optic probe to differentiate between phenotypes. The combined effect of high glycogen and low protein content in the meat was consid-

ered to make it possible. The NIR measurements could be performed already 30 min. post mortem. Only four non-carriers were misclassified as carriers of the *RN* allele, which gave 4% misclassified samples in total. In comparison with the analysis of glucose and glucose-6-phosphate in meat juice, the NIR method can be performed early post-mortem.

Detection of the *RN* Mutation and Physiological Effects of the Gene

The *RN* allele was mapped on chromosome 15 (Mariani et al., 1996; Milan et al., 1996), and before the identification of the *RN* mutation a number of markers were used for genotyping the *RN* allele (Looft et al., 2000). A close collaboration between scientists in France, Germany and Sweden made it possible to identify the *RN* mutation (Milan et al., 2000). It was shown that the mutation was a substitution in the *PRKAG3* gene, which encodes a muscle-specific isoform of the regulatory γ subunit of adenosine monophosphate-activated protein kinase (AMPK). The function of the gene is still not fully known, but loss of function mutations in a homologous gene in yeast (*SNF4*) causes defects in glucose metabolism, including glycogen storage. Mammalian AMPK is important for regulation of energy metabolism. Activated AMPK is expected to inhibit glycogen synthesis and stimulate glycogen degradation. AMPK also leads to translocation of glucose transporter 4 (GLUT4) from an intracellular location to the plasma membrane, increased glucose uptake and increased glycogen content in skeletal muscle (see Milan et al., 2000 for references). In the paper by Milan et al. (2000) the authors found that the AMPK kinase activity in muscle extracts was about three times higher in normal *rn+* pigs than in *RN* pigs. The authors suggest that the *RN* mutation could be a dominant negative mutation inhibiting AMP activation and glycogen degradation. It can also be a gain-of-function mutation, leading to an increased glucose transport and/or glycogen synthesis. Then, the reduced AMPK activity in *RN* pigs might reflect feedback inhibition due to the high-energy status of the muscle.

The *RN* mutation has only been found in Hampshire pigs or crossbred pigs including Hampshire with high glycogen content, and not in any other pig breed (Milan et al., 2000). Due to the negative effect of the *RN* allele on technological meat quality, most countries and breeding companies would like to eliminate the mutation. With the mutation identified this can easily be achieved. However, the positive effects of the *RN* allele on eating quality should be considered.

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