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THE BUFFERING CAPACITY OF PORCINE MUSCLES

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Abstract

The aim of this study was to investigate the buffering capacity (BC) of five porcine muscles. The pH of muscles with zero lactate was also estimated. The BC was calculated on the basis of the amount of lactate accumulating in the muscle between two sampling times and the simultaneous pH decline. Two muscle samples were obtained from each muscle (n=13-36):

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one as soon as possible after slaughter and the other 24 h *post-mortem*. The BCs (mmol lactate/(pH*kg)) were in the light *gluteus superficialis*, *longissimus dorsi* and *semimembranosus* muscles 48.3 ± 8.8 , 48.6 ± 9.2 and 46.8 ± 13.0 , and in the dark *infraspinatus* and *masseter* muscles 45.3 ± 13.1 and 32.0 ± 11.5 , respectively. The dark *masseter* muscle differed significantly from the other muscles studied ($p < 0.01$). The estimated pH values of muscles with zero lactate were in the *gluteus*, *longissimus dorsi*, *semimembranosus* muscles 7.14 ± 0.06 ; 7.18 ± 0.06 ; 7.38 ± 0.08 , and in the *infraspinatus* and *masseter* muscles 6.87 ± 0.07 ; 7.03 ± 0.08 , respectively. It was suggested since lactate is continuously formed in the muscles, the resting pH of living light and dark muscles may, however, be the same. The approach used in this study to determine the BC resulted in values which are close to values previously reported in the literature (measured by using titration curves).

Keywords: Muscle; Pig; Buffering capacity; pH

1 Introduction

The chain of events that leads to the conversion of muscle to meat is complex, and it involves a series of biochemical reactions in the muscle fibre, resulting in conformational changes in the myofibrillar system. As a result of *post-mortem* metabolism, glycogen and ATP levels decline, and lactic acid accumulates in the muscle. This lowers the muscle pH (Kastenschmidt, Hoekstra & Briskey, 1968) and results in an ultimate pH of about 5.4 to 5.7 at 24 h in porcine *longissimus dorsi* muscle (Briskey & Wismer-Pedersen, 1961). The amount of glycogen present in the muscle will determine the extent of the pH decrease, but only if the glycogen concentration in pig muscles has decreased to values below 53 mmol/kg wet weight in the living animal (Henckel, Karlsson, Jensen, Oksbjerg, & Petersen, 2002). The pH has a

direct or indirect influence on several characteristics of meat, such as colour, water-holding capacity, tenderness, juiciness and flavour (Kauffman et al., 1993). The effects of pH on meat quality have been thoroughly reviewed e.g. by Hamm (1972), Bendall & Swatland (1988) and Offer & Knight (1988).

The fall in pH during the *post-mortem* reaction sequence is a function of both the amount of acid formed and of the buffering capacity (BC) of muscle (Bate-Smith, 1938; Kivikari, 1996, review). In chicken *pectoralis* (van Laack, van Liu, Smith & Loveday, 2000) and in pork *longissimus dorsi* (van Laack & Kauffman, 1999), muscles with equal lactate content may have different ultimate pH values. This may be explained by differences in buffering capacity (van Laack, Kauffman & Greaser, 2001).

Buffering capacity is the ability of meat to resist the change in pH when acid or alkali is added. Usually the buffering capacity of meat is measured using titration curves (Kivikari, 1996, review). The measure for the buffering capacity, β , is the slope of the titration curve (pH plotted against increments of alkali or acid) at any point; $\beta = \delta A / \delta pH$, δA = the amount of added acid/alkali, δpH = the corresponding change of pH.

The value of K_a for lactic acid is 1.38×10^{-4} . Theoretically, adding lactic acid (10 mmol) to pure water (1 dm³) causes the pH to fall from 7.00 to 2.93. The buffering capacity of muscles balances the pH change and prevents the rapid pH decrease followed by rapid glycolysis. Buffering capacity is an important property of both living muscle and *post-mortem* meat. The same chemical compounds that regulate pH in a living muscle fibre also regulate it *post-mortem* (Kivikari, 1996, review).

Several values (which differ from each other according to the dilution ratio used in titrations) have been presented for the BC of porcine muscles: for *psoas* 57 mmol H⁺/pH*kg (pH 6-7) (Bate-Smith, 1938), for *longissimus dorsi* 55 mmol H⁺/pH*kg (pH 5.2-6.5) (Sayre, Briskey & Hoekstra, 1963), 57 mmol H⁺/pH*kg (pH 5.2-6.5) (Monin & Sellier, 1985), 60-64 mmol H⁺/pH*kg (pH 6-7) (Henckel, Jörgensen, & Jensen, 1992), 52 mmol H⁺/pH*kg (pH 5.5-7.0) (Puolanne & Kivikari, 2000), for *adductor* 50 mmol H⁺/pH*kg (pH 6-7) (Castellini & Somero, 1981) and for *triceps brachii* 45 mmol H⁺/pH*kg (pH 5.5-7.0) (Puolanne & Kivikari, 2000).

Buffering capacity is a function of pH. The most influential compounds in the pH range of 5.5-7.0 are phosphate compounds having pK_a values between 6.1 and 7.1, the dipeptides carnosine and anserine, and histidylimidazole residues of myofibrillar proteins (Kivikari, 1996, review). Myofibrillar proteins are responsible for approximately half of the buffering capacity of meat in the pH range 5.5-7.0 (Honikel & Hamm, 1974). Different phosphate compounds have different pK_a values, and during the *post-mortem* reaction sequence, the buffering capacity of each compound changes, depending on how its pK_a value is related to the pH value of meat (Kivikari, 1996, review). As a result, there are minor differences in *pre rigor* and *rigor* buffering capacities. According to Kivikari (1996) the difference in BC during the *post-mortem* reaction sequence is approximately 8 mmol H⁺/(pH*kg) at the maximum point of the curve. This is caused mostly by free phosphate ions.

Puolanne & Kivikari (2000) found that the dilution ratio affects the BC curves determined by titration. With a dilution ratio of 10/100 they found a maximum buffering capacity of 65.4 mmol H⁺/pH*kg at pH 6.65 and a minimum of 38.9 mmol H⁺/pH*kg at pH 5.56 for porcine *longissimus dorsi* muscle. The equivalent BCs with a dilution ratio of 10/10 were 57.2 mmol H⁺/pH*kg at pH 6.69 and 48.9 mmol H⁺/pH*kg at pH 5.70, respectively. They

assumed that the less water used in the determination of the BC curve, the more the curve takes on a shape with no separate maximum or minimum. According to Puolanne & Kivikari (2000) the most probable consequence of this is that when no added water is used in the titration, the buffering capacity is constant in a pH range of approximately 5.8-6.5. The BC has also been determined without dilution (e.g. Bendall, 1973; Bendall, 1979; Talmant, Monin, Briand, Dadet & Briand, 1986; Guignot, Quilichini, Renerre, Lacourt & Monin, 1992), but information on the BC of intact *post-mortem* meat is insufficient.

Muscles can be classified into dark and light types, which differ on the basis of their fibre composition. Most muscles have a fibre composition which is a mixture of light and dark fibres. The BC is found to be higher in light anaerobic muscles than in dark ones (Davey, 1960; Rao & Gault, 1989; Okuma & Abe, 1992; Kivikari, 1996). In living muscles, dark fibres tend to maintain their energy-rich phosphate levels aerobically, but light fibres have a stronger aptitude to maintain their ATP supply anaerobically, and the formation of lactic acid (Fernandez, Tornberg, Naveau, Talmant & Monin 1992; Henckel et al., 2002) tends to lower the pH value in the fibre (Olsman & Slump, 1981). Many of the treatments which living animals are exposed to have a strong impact on muscle metabolism and, therefore, the measuring of the pH value of living muscle is difficult (Roos & Boron, review 1981). The situation where there is zero lactate in muscle, may offer valuable information about differences between muscles.

Somero (1986) states that a high buffering capacity in muscle stabilises intramuscular pH and enhances the capability for anaerobic metabolism. Differences in the BC of the various muscle types can be explained by variations in dipeptide, mainly carnosine, anserine (Kivikari, 1996, review) and balenine (β -alanyl-3-methyl-histidine) contents (Olsman & Slump, 1981).

The aim of this study was to examine the actual (i.e. without any dilution) buffering capacity of porcine muscles *post-mortem*. In this study, the BC was calculated on the basis of lactate accumulation in the muscle, in relation to the change in pH value during 24 h after slaughter. The pH values of muscles with zero lactate were also estimated.

2 Materials and methods

2.1 Animals and sampling

Muscles of Finnish Landrace and Large White pigs and their crosses were used. The pigs were slaughtered at the age of 165 ± 2 days. The live weight of the pigs ranged from 86.0 to 118.5 kg. On the day of slaughter, the pigs were transported (approximately 1 h), two at a time, to a pilot abattoir. They were allowed to rest for 2 h before slaughter and then stunned electrically.

Samples were taken from light *gluteus superficialis* (25-30 min pm), *longissimus dorsi* (15-18 min pm), and *semimembranosus* (about 40 min pm) muscles and from dark *infraspinatus* (15-18 min pm) and *masseter* (15-18 min pm) muscles. The numbers in parentheses indicate sampling time 1 (ST1) after the stunning. The number of muscle samples varied between 13 and 36 (see Table 1). The next samples were taken 24 h *post-mortem* (ST2). The elapsed time between the sampling times was long because the animals were also used in a different study. The samples were cut into small pieces and frozen in liquid nitrogen. Freezing took place within 1 min after sampling. The samples were stored at -80°C until they were used for the analyses.

2.2 Measurements

The pH values were measured in meat extracts (1 g muscle + 10 ml 5 mM Na-Iodoacetic acid solution) by using a Knick Portamess 752 pH-meter equipped with a Mettler-Toledo Inlab 427 electrode. Extracts were made from muscles which were frozen just after the sampling (pH_{ST1}), and from samples which were frozen 24 h *post-mortem* (pH_{ST2}). The frozen samples were homogenised in icy Na-Iodoacetic acid and the pH values were measured at room temperature.

For lactate determinations, muscle samples were homogenised in ice-cold 0.1 M phosphate buffer (pH 7.0) with a Polytron homogenizer. Lactate concentration was determined spectrophotometrically (365 nm) using a commercial kit (Boeringer-Mannheim no. 139 084).

The reproducibility of the lactate assays was determined as follows: a large muscle sample was ground in liquid nitrogen, divided into small pieces and stored at -80°C . This sample was analysed every time the samples were analysed. The coefficient of variation (CV) was $\pm 12.5\%$ for the lactate analyses.

The total pigment content was first analysed with Trout's (1991) method and the relative amount of myoglobin was determined electrophoretically by the Pharmacia separation technique (Phasta SystemTM, 1989).

The buffering capacity of each muscle sample was calculated as described by Hill, Irvine and Bullock (1985), i.e. based on the amount of lactate accumulating in the muscle between the first and second sampling and the simultaneous pH decline:

$$BC = \Delta A / \Delta pH,$$

where ΔA is the observed increase of lactate (mmol); and ΔpH is the change in pH of muscle.

2.3 Statistical analysis

The statistical analysis was carried out with the Statistical Analysis System version 6.12 (SAS, 1990). The MIXED procedure was applied when calculating the least squares means of all the variables. The REG procedure was applied when the pH values of muscles with zero lactate were estimated.

3 Results and discussion

3.1 Lactate production, pH value and the buffering capacity of the muscles

The myoglobin contents (mg/g) were 5-6 times higher in the dark *infraspinatus* and *masseter* muscles (11.2 ± 3.4 and 11.6 ± 1.4 , respectively) than in the light *gluteus*, *longissimus dorsi* and *semimembranosus* muscles (2.6 ± 0.5 , 1.8 ± 0.4 and 2.2 ± 0.6 , respectively). This is consistent with the results of Morita, Cassens, Briskey, Kauffman & Kastenschmidt (1970) and Livingston & Brown (1981), who found that dark muscles contain more myoglobin than light ones.

As compared with the dark muscles, the pH_{ST2} of the light muscles was significantly lower ($p < 0.001$) and there was significantly more lactate at 24 h after slaughter ($p < 0.001$) (Table 1). Fernandez & Tornberg (1991) have reported that the ultimate pH differs in different types of

pig muscles, basically because light muscles contain more initial glycogen than dark muscles (Monin, Mejenes-Quijano & Talmant, 1987). This was also the case in this study, although the results of glycogen content are not shown.

In the *semimembranosus* muscle the lactate content was higher and the glycogen content lower (Ruusunen & Puolanne, 2003) than in the other light muscles studied (Table 1). This may be due to the differences in sampling time, since the sample from the *semimembranosus* was taken later than from the other muscles. Because of the differences in ST1, it is not reasonable to compare the pH and lactate values directly. The aim of this paper is to compare the ratio of lactate content and pH between different muscles. The differences in lactate content or pH at ST1 are not of importance as absolute values.

The pH_{ST1} (Table 1) was different only between the *semimembranosus* and the *masseter* muscles. The fact that the pH_{ST1} was not different for most muscles, despite differences in the lactate content at ST1, could be attributed to the higher buffering capacity of the light muscles, which has been shown earlier by Rao & Gault (1989).

The average BC in the particular pH range (from pH_{ST1} to pH_{ST2}) of each individual muscle sample was calculated on the basis of lactate accumulation in the muscle in relation to the simultaneous change in pH value. The means and standard deviations of these results are presented in Table 1. The BC was different in different muscles and the trend indicated a higher buffering capacity in the light muscles than in the dark ones. There was a significant ($p < 0.001$) difference between the BCs of dark *masseter* muscle and the light muscles studied, but the BC of the *infraspinatus* muscle seemed to be at the same level as that of the light muscles.

The buffering capacities of light muscles (Table 1) are at the same level as the mean BC value of Puolanne & Kivikari (2000): 52 mmol H⁺/(pH*kg) for porcine *longissimus dorsi* muscle (estimated from titrations made with dilution ratios of 1:10 and 1:1) when the pH range was from 5.5 to 7.0. The BC of the *masseter* muscle was lower than of that of the *infraspinatus* muscle and the same as (Table 1) the mean BC value of Puolanne & Kivikari (2000) for porcine dark *triceps brachii* muscle: 45 mmol H⁺/(pH*kg). Furthermore, Guignot et al. (1992) have determined the buffering capacity of three different veal muscles with titration and also with the method used in this study and obtained values which were very close to each other.

Buffering capacity remains constant over a certain pH range only if the titration curve over the same pH range is linear. Hamm (1977), however, has pointed out that a linear relationship between the linear magnitude of lactate concentration and the logarithmic magnitude of pH is by no means self-evident. However, in meat samples the correlation between lactic acid concentration and pH value can be considered as linear or almost linear because the pH-lactate curve in the pH range 5.5-7 represents the almost linear medium part of the titration curve (Hamm, 1977). The pH values of muscles in this study were close to this range and BC could be considered constant. There are differences in *pre rigor* and *rigor* BC. As mentioned in the introduction, these are caused mostly by free phosphate ions, but the differences are small (Kivikari, 1996) and do not have a marked effect on the results. This is because at ST1 the number of free phosphate ions in the muscle has not increased markedly, and at ST2 they have only a marginal effect.

Puolanne & Kivikari (2000) found that the dilution ratio affects the BC curves determined by titration. They assumed that the less water used in the determination of the BC curve, the more the curve has a shape with no separate maximum or minimum, and the most probable consequence of this is that when no added water is used in the titration, the buffering capacity

is constant in a pH range of approximately 5.8-6.5. In this study the BCs were determined without dilution, and this approach resulted, as expected, in slightly lower values than presented earlier in the literature.

3.2 The calculated pH of muscle with zero lactate

The pH of muscle with zero lactate was extrapolated by fitting a linear regression model to the data obtained from ST1. In this study it was assumed that the BCs of the same muscle of each animal were approximately equivalent. The assumption was based on the fact that the animals were from the same genetic line, reared similarly and gave the BC results presented above. There were, however, some unexpectedly high differences in the data; sometimes the pH value showed large variations at the same lactate content (Figs. 1 (a)-(e)).

The extrapolated values of the pH of a muscle with zero lactate ($\pm$ standard error) in the light *gluteus*, *longissimus dorsi* and *semimembranosus* muscles were 7.14 ± 0.06 ($r=0.88$), 7.18 ± 0.06 ($r=0.90$) and 7.38 ± 0.08 ($r=0.90$) and in the dark *infraspinatus* and *masseter* muscles 6.87 ± 0.07 ($r=0.65$) and 7.03 ± 0.08 ($r=0.73$), respectively. The coefficients of correlation were not very good in the dark muscles, the possible result being a pH value that is slightly too low, especially in *infraspinatus* in a zero lactate situation. Nevertheless, the difference between the light and dark muscles remains, though the difference may be smaller. The low coefficients of correlation were probably due partly to the smaller range of variation in the lactate content and pH value of the dark muscles. Furthermore, dark muscles are not as homogeneous as the light muscles.

Also Renou, Canioni, Gatelier, Valin & Cozzzone (1986) extrapolated initial pH value (pH at the time of slaughter) by fitting a linear regression for rabbit *psoas major* muscle, and

obtained a value of 7.14, which is in agreement with our results and also with Bendall's (1975) results for the initial pH values porcine *semimembranosus*, *longissimus dorsi* and *gluteus medius* muscle: 7.16, 7.16 and 7.24, respectively.

Kivikari (1996) estimated that the pH value of living muscles (*M. longissimus dorsi*, *M. triceps brachii*) for pork and bovine is 7.2 and for broiler (breast muscles, leg-thigh muscles) 7.6, the latter being unexpectedly high. Our extrapolated results for light porcine muscles were in agreement with Kivikari's (1996) results. In the dark muscles the pH was lower than in Kivikari's study.

Fernandez et al. (1992) and Henckel et al. (2002) have studied the *longissimus dorsi* muscle of a resting pig using biopsy sampling, and found a lactate content of about 5 and 11 mmol/kg muscle wet weight, respectively. Sepponen, Koho, Puolanne, Ruusunen & Pösö (2003) have speculated that because both the capillary and mitochondrial densities are low in porcine muscles, small amounts of lactate are continuously formed as a result of anaerobic glycolysis. Considering that there is always some lactate in the muscle, the resting pH of porcine *longissimus dorsi* muscle of a living animal in this study is about 6.95-7.07. Also, Tarrant, McLoughlin & Harrington (1972) have measured an initial pH value of 7.0 ± 0.03 for living anaesthetised porcine *longissimus dorsi* muscle and assumed that this value was probably close to the pH of resting, normal muscle.

In muscle, the major portion of carrier-mediated lactate transport occurs via the function of monocarboxylate transporters (MCT), which transport a lactate anion and a proton together in the direction of a declining lactate gradient (Juel, review 1997). Sepponen et al. (2003) found that MCT2 along with MCT4 appear to be the major isoforms in both the dark and the light porcine muscles and that the amount of MCT2 is higher in light porcine muscles than in dark

ones. Because light muscles are more glycolytic than dark ones (Briskey & Wismer-Pedersen, 1961; Merkel, 1971; Lundström, Essén-Gustavsson, Rundgren, Edfors-Lilja & Malmfors, 1989; Warner, Kauffman & Russell, 1993), it can be assumed that there is already more lactic acid in living light muscle than in dark muscle. This would induce a problem because all muscles consist of light and dark muscle fibres, and an existence of a pH gradient between light and dark fibres would not be energetically favourable and would lead to ion exchange. Our finding that pH of light muscles with zero lactate is higher than that of dark muscles suggests that adjacent muscle fibres may have different energy metabolisms. Because in light muscles lactic acid is continuously formed more than it can be utilised [based on the resting lactate content found by Fernandez et al. (1992) and Henckel et al. (2002)], the lactic acid formed must be transported out of the fibres. Sepponen et al. (2003) suggest that in glycolytic porcine fibres, lactate concentration could be kept at a low level by the function of MCT2. The lactic acid is transported from light fibres to dark fibres, which have a higher capacity to use it for energy production (Juel, review 1997). Because of the difference in pH between light and dark muscle fibres with zero lactate, it would be possible to continuously produce lactic acid in light muscle fibres and transport it via interstitial space to dark muscle fibres without developing a disadvantageous pH gradient.

On the basis of the above information, we suggest that because there is more lactic acid in light muscle fibres than in dark ones, the pH with zero lactate must be higher in light fibres than in dark fibres to avoid the development of an energetically unfavourable pH gradient between these fibres. Consequently, the resting pH of living light and dark fibres can be the same. However, more research on the pH value of adjacent muscle cells is needed.

4 Conclusions

This study points out that the buffering capacity calculated from the lactate accumulation and the simultaneous pH decrease in muscle, i.e. without dilution, gives results which are close to the values determined with the titration method and reported in the literature. The method is also rapid and easy to carry out. The buffering capacities are higher in light porcine muscles than in dark porcine *masseter* muscle. The estimated pH value of light muscles with zero lactate is higher than that of dark muscles. It was suggested that since lactate is continuously formed in the muscles, the resting pH of living light and dark muscles may, however, be the same.

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Legend to the figure

Figures 1 (a)-(e). The pH at ST1 of light *gluteus*, *longissimus dorsi*, *semimembranosus* muscles and dark *infraspinatus* and *masseter* muscles in relation to lactate content. N.B. The x-axis of light muscles is to 120 mmol/kg and of dark muscles to 60 mmol/kg.

Table 1. LSMeans and standard deviations of pH_{ST1}, the lactate concentration at first sampling, pH_{ST2}, the lactate concentration at second sampling and BC in different porcine muscles.

	pH _{ST1}	Lactate _{ST1} mmol/kg	pH _{ST2}	Lactate _{ST2} mmol/kg	BC mmol LA/(pH*kg)
<i>gluteus superficialis</i>	6.46±.20ab n=36	53.2±14.7a n=36	5.48±.08a n=36	101.4±6.4a n=36	48.3±8.8a n=36
<i>longissimus dorsi</i>	6.43±.22ab n=36	56.3±14.3ab n=36	5.45±.06a n=36	104.6±7.7a n=36	48.6±9.2a n=36
<i>semimembranosus</i>	6.37±.28a n=36	61.9±15.0b n=36	5.46±.09a n=34	104.9±8.3a n=34	46.8±13.0a n=34
<i>infraspinatus</i>	6.48±.12ab n=35	36.7±8.5c n=35	5.89±.16b n=14	66.1±9.2b n=14	45.3±13.1ab n=13
<i>masseter</i>	6.53±.11b n=36	31.7±5.5c n=36	5.95±.07b n=16	55.6±3.7c n=16	32.0±11.5c n=16
significance	**	a&b* a&c, b&c***	***	***	a&c*** b&c*

Means in columns with the same superscript are not significantly different at the 5 % level

*** p<.001, ** p<0.01, * p<.05