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The effect of pre-treatment of pigs with curare on the post-mortem rate of pH fall and onset of rigor mortis in the musculature

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The post-mortem rate of pH fall in the muscles of various breeds of pig has been shown by numerous workers to be extremely variable from animal to animal (c.f. Bendall and Lawrie, 1964, for a review, and the papers of Ludvigsen 1954, Briskey et al, 1959 and Wismer Pedersen and Briskey, 1961). This is true, not only of muscles on the carcase under factory conditions, where the pH_1 value at 45 mins after death is a guide to the rate, but also of isolated pieces of muscle kept in the laboratory at constant temperature (c.f. Bendall et al. 1963: Sayre and Briskey, 1963). Since the higher rates of pH fall are generally associated with the more or less severe occurrence of so-called pale, watery pork, when the carcase is examined the next day, this phenomenon is of considerable commercial importance, and it is essential to discover its underlying cause. It seems certain from the studies of Wismer-Pedersen and Briskey, that among the contributory causes are excitement and fighting before death, one way of avoiding the former being to cool the pig down in a bath of water. (Kastenschmidt, Briskey and Hoekstra, 1964). Briskey and his co-workers showed that this treatment had the rather surprising effect of reducing the deep muscle temperature after slaughter, but it seems unlikely that the rather small temperature differences observed are sufficient to explain the subsequent very large differences in rates of pH fall.

Another way of looking at the phenomenon is to suppose that the excessive numbers of nervous stimuli, which reach the muscles in an excited pig just before it is killed, and which possibly lead to local anoxia in such a badly trained animal as a result of the contractions they produce, not only have the short term effect of causing a large local production of lactic acid, that is, a low initial pH, but also a long term effect on the rate of this production. Hallund and Bendall (1965) have indeed been able to demonstrate just such an effect by comparing the rate of pH fall in excised pieces of muscle, exposed to a brief tetanus, with that in unstimulated controls, kept under anaerobic conditions at 37°C.

It turned out to be very difficult, however, to obtain muscles of sufficiently high initial pH from the Danish Landrace pigs used in the work, hence the present study was undertaken of the effect of completely immobilising the pigs before death with curare. This had the expected effect of giving very high and regular initial pH values, and a very low rate of pH fall in the longissimus dorsi muscles (LD). The pH/time curve was in fact even more long drawn out than that observed in the psoas muscles of rabbits, immobilised before death with myanesin, which had previously been found to be among the slowest of the species then investigated (c.f. Marsh 1954, Bendall and Lawrie 1962).

Direct tetanic stimulation of the muscles from pigs immobilised in this way had the immediate effect of causing a slight fall of pH of less than 0.15 pH unit, and the long term effect of increasing the rate of pH fall to nearly twice the control value during the next 2 hours or so. This accelerating effect of stimulation under anaerobic conditions cannot be attributed to the loss of creatine phosphate (CP) or of adenosine triphosphate (ATP), due to the powerful tetanic contraction which takes place, because such loss is only small. It must therefore be due to a long-term effect on the systems which control the rate of ATP-turnover in the muscle, because it is on the latter that the rate of lactic acid production and of pH fall, post-mortem, primarily depend. (Bendall 1960). The implications of this are discussed more fully in the paper.

METHODS

A group of 10 Large White pigs from the experimental stock of the Institute for Animal Physiology at Babraham was chosen for the experiments. The weights varied between 80 and 90 kilos. This breed was used, because the rate of pH fall in its LD muscles had been found to be the lowest of any (Lawrie 1960), and the effect of stimulation could therefore be expected to be most easily detectable.

Curarised Pigs.

Six of the pigs were immobilised by injection of curare in the following way:- The animal was first injected intramuscularly, with 250 mg. of the tranquilliser, phencyclidene. 30 mins later it was injected intravenously with 1.2 g. nembutal in 20 ml., and as soon as the anaesthetic had taken effect, the trachea was exposed and opened, and a rubber tube with cuff inserted. The tube was connected to a

closed circuit oxygen apparatus and the respiration checked by means of a bag. 10 mg. of tubocurarine chloride in 1 ml. were then given intravenously. Spontaneous respiration ceased almost immediately after the injection, but the heart rate was unaffected. The animal was immediately put on assisted breathing, from the bag by hand, and then a further 10 mg tubocurarine chloride was given i.v. to ensure complete relaxation of the musculature. The operations were kindly performed in the post-mortem room of the Institute at Babraham by Dr. B.A. Baldwin, except the injection of curare which was given by me (J.R.B.).

10 mins after the last injection of curare, the animal was hoisted by a hind leg, in the usual manner, and killed by slitting its throat. An incision was then made along the skin of the spine from the middle of the thorax to the last rib, and a 25 cm long portion of the LD muscle carefully dissected out through it, and taken back as quickly as possible to LTRS, Cambridge.

Two portions, about 7 cms long by 8 cms wide by 2 cms thick, were cut from the freshly excised muscle, parallel to the axis of the fibres, about 25 mins. after death. From one portion, unstimulated, a 1 g. sample was taken for measurement of pH at 20°C, after homogenisation in 5 ml of 5 mM sodium iodoacetate. In two of the pigs, a further 1 g. sample was taken from the unstimulated piece for homogenisation in 4% perchloric acid, and subsequent estimation of CP, ATP and inosine monophosphate (IMP) by the methods of Bendall and Davey (1957). The other portion was placed between two stainless steel plates, connected to the poles of a motor cycle magneto, and tetanised in two bursts of 10 secs. each. 1 g. samples were then cut from this piece for the measurement of pH and ATP etc. as above. After cutting the initial samples, the unstimulated and stimulated portions were wrapped in polythene bags and placed in a cabinet at 38°C. 1 g. samples for pH and chemical estimations were removed at the intervals shown on the various figures.

The time course of rigor was followed by the change of extensibility of a strip taken from the unstimulated muscle, by the method of Bate-Smith and Bendall (1948), except that the strip was tied at each end with cotton thread, instead of tape, and suspended in a bath of liquid paraffin, attached to the kymograph apparatus in a room at 38°C.

Control Pigs. 4 of the pigs were used as controls, and were slaughtered in the normal manner, by electrical stunning and sticking. LD muscle was removed through an incision in the back and samples taken at intervals for pH measurements, as above. The muscle samples were kept in a cabinet at 38°C until rigor was complete. In two cases, the time-course of rigor mortis was measured in a strip on a kymograph in a room at 38°C.

RESULTS

The average pH/time curves for the unstimulated and stimulated muscles from curarised animals, and the unstimulated muscles from electrically stunned animals, are shown in fig. 1, where the vertical bars at the times shown indicate the corrected standard errors for 6 measurements in each case. Also shown is the average curve for the loss of extensibility in the unstimulated muscles from the curarised animals. It is seen that the initial pH in the curarised muscles must have been very high, because it is still 7.23 at 30 mins. after death. The immediate effect of the stimulation (group 2) has been to lower the pH by about 0.14 units, which in terms of time represents a loss of about 25 mins, whereas the long term effect has been to increase the rate of fall, mostly in the pH range between 7 and 6, so that the time taken to reach pH 6 is only 210 mins compared with about 360 mins. for the unstimulated muscles. In terms of rates over this range of pH, those for the stimulated muscles are 1.7 times those for the unstimulated. It is also obvious from the magnitude of the standard errors that there is no possibility of curves 1 and 2 being coincident at any point except at the start and the end. The average ultimate pH in both cases was 5.40 $\pm$ 0.02 (n = 10).

The situation with muscles from pigs stunned and stuck in the normal way (curve 3) is very different. As might be expected, the major effect of the unavoidable struggle during slaughtering has been to lower the initial pH drastically (6.7 at 30 mins. after death), but unlike the value for the curarised animals, this has a very high standard error ($\pm$ 0.09 for n = 6), reflecting the large variability always observed in pigs killed in this way. The subsequent course of the pH/time curve is, however, not dissimilar from that for the curarised animals (curve 1), although the variability from animal to animal is again high, as shown by the standard errors. Because of this, the curve tends to become

confused with that of the stimulated, curarised muscles at pH values below pH 6.2. The ultimate pH, as would be expected, is close to that of the curarised muscles (5.48 ± 0.04 for $n = 4$).

A feature of the muscles from normally slaughtered animals which is obscured in the average pH/time curves shown in fig. 1, is the variability of pH within the piece of muscle from which the samples were taken. We often find, for instance, two very different, although self-consistent, pH/time curves for samples from each end of the piece, as illustrated for two pigs in fig. 2. Apparently these represent the variability between different groups of fibres within the same muscle, and therefore the change in extensibility, which is measured by stretching another group of fibres in a thin adjacent strip of muscle, may follow the time course of either, or an intermediate one. In fig. 2a, for instance, the time course of the extensibility change is closer to the slower of the two pH/time curves, whereas in fig. 2b it is closer to the faster. Such variability, not only between animals, but even within the same piece of muscle, makes it difficult to generalise, except in so far that the time course of both the pH and extensibility changes is always faster in such muscles than in unstimulated curarised ones. It is also seen that the highest rates of pH fall observed in the non-curarised muscles (for example, the faster of the two curves in fig. 2a) are higher even than the average rate for the stimulated curarised muscles (fig. 1, curve 2). The absolute average rates from pH 7 to 6 are 0.21 pH units per hour for unstimulated curarised and 0.36 units per hour for stimulated curarised muscles, compared with a maximal rate of 0.51 units per hour in fig. 2a.

Fig. 3, a and b, illustrates the time-course of the changes in CP and ATP content in stimulated and unstimulated muscles from 2 curarised pigs. The change of extensibility is also shown for one of the unstimulated muscles, and is seen to follow very closely the changes in ATP. It will be noted that there is a similar difference between the time-courses of these chemical changes in the stimulated and unstimulated muscles, as there is in those of the pH changes illustrated in fig. 1, although these two particular pigs showed slower changes than the 4 others in the group. Thus the time for half change of ATP in the unstimulated muscles is about 360 mins. against 190 mins. in the stimulated muscles.

Stimulation has also had the effect of lowering the initial level of CP, but not that of ATP, and also of accelerating the rate of CP breakdown, although the time difference caused by these effects is by no means as great as the difference in times of half change of ATP. We did not analyse the chemical changes in the non-curarised muscles, because these have already been exhaustively studied (Bendall et al. 1963; Lawrie 1960; Sayre and Briskey 1959), and we would expect the general pattern to be the same as that noted by these authors.

To demonstrate that the effects of stimulation described here are qualitatively and almost quantitatively the same as those described by Hallund and Bendall (1965) in the muscles of the Danish Landrace breed, we have corrected the pH/time curves of one of the curarised Large White pigs (pig 6) for differences in initial pH, and superimposed on them the average pH/time curves given by the above authors for their stimulated and unstimulated groups of muscles (see fig. 4). It will be noted that the agreement is remarkably good, although it is obvious that curarisation has slowed down the changes in the unstimulated muscle, particularly in the pH range between 6.5 and 5.8, presumably because it has prevented any nervous stimuli whatever from reaching the muscle during slaughter, whereas the muscles of the Danish pigs, which were killed in the normal way, were fully exposed to this hazard.

In this connection, it is also worthwhile recording the results of the effect of immobilisation of two Danish Landrace pigs with the motor horn-cell paralysant, myanesin (unpublished results of Hallund and Bendall), because they illustrate rather well the essential similarity of the time course of rigor mortis in all pigs of whatever breed, when nervous stimuli cannot reach the muscles during slaughter. (fig. 5). We have superimposed (for comparison) the average curves of the six curarised pigs, after adjustment for the differences in initial pH; the latter is rather lower in the Danish pigs (7.0) than in the English (7.30), because myanesin is not as effective a relaxant as curare. It will be noted that the pH changes are slightly faster in the Danish pigs than in the English (225 mins. to reach pH 6.0, against 250 mins.), whereas the position is, for some reason, reversed in the case of the extensibility changes.

The time course of the various physical and biochemical changes in different species are summarised in table 1.

DISCUSSION

The purpose of the present paper was to demonstrate that the long-term accelerating effect of electrical stimulation on the post-mortem changes in excised pig muscles, which has been described by Hallund and Bendall (1965) in the case of Danish Landrace pigs, was a general phenomenon and also applied, for instance, to English Large White pigs, immobilised by curare before death. The latter pre-mortem treatment has the advantage that no nervous stimuli can reach the muscles during slaughter, so that the initial pH, CP and ATP values are high and reasonably constant from animal to animal. In this way, we have a baseline, as it were, of slow post-mortem change, over the whole range of pH which can be traversed in the muscles of a well fed pig, similar to that obtained earlier (Bendall 1951) for the muscles of rabbits immobilised with myanesin. Thus not only is any post-mortem treatment, such as stimulation, likely to have its maximal effect, but we also have a standard with which to compare the extremely variable material frequently obtained in normal slaughter-house practise.

As it turns out, brief tetanisation of curarised muscles from Large White pigs has very similar effects, qualitatively and quantitatively, to those described earlier for the untreated muscles of Danish Landrace, but over a wider range of pH. In both cases, the immediate effect of stimulation is to lower the pH by about 0.15 units and the CP content by about 10%, without affecting the ATP content. These immediate effects, however, are quite insufficient to explain the long-term accelerating effect on all the post-mortem changes investigated. As shown in table 1, stimulation nearly doubles the rate of pH fall over the range 7 to 6, and halves the time for half-change of ATP. Possible mechanisms by which it does so have been discussed by Hallund and Bendall (1965) and will be touched on later here, but the bearing of the effect, as an empirical finding, on the well-known variability of pH fall in pig muscles is obvious.

When a pig is killed by the usual slaughterhouse procedure, there are several factors which all tend to produce a high lactic acid content in its muscles. First there is the tension and excitement of the journey and in the holding pens; then there is the chase to stun it or shackle it, which is likely to cause a more or less severe oxygen debt in such an untrained animal as the pig; then there is the electrical stunning itself, which causes tension and twitching in the muscles; and lastly there is the vigorous kicking and arching of the back, which often ensues

after the throat has been cut. It is no wonder then, that initial pH values are extremely variable, even within quite a small area, in muscles such as the LD (c.f Hallund and Bendall, 1965, for example, and fig. 2 of this paper). Very similar variability is found in the psoas muscles of rabbits, killed by a blow on the head, or of beef animals, slaughtered in the usual way, because these muscles are particularly involved in the spontaneous kicking of the hind legs, which occurs after death. Where the pig differs from the other animals, however, is that the very stimuli which produced the low initial pH are also likely to lead to a long-term acceleration of all the post-mortem biochemical changes, in just the same way as artificial electrical stimulation does. In fact, the initial pH is itself an indirect measure of the intensity of the stimuli which reached the muscles before and during slaughter, in the sense that the lower the pH, the more intense the stimuli must have been, and therefore the greater their long-term accelerating effect on the biochemical changes.

As an example of the extremes which may occur in practise, let us suppose that the pH immediately after death in the LD of one pig happened to be as low as 6.3, indicating severe nervous stimulation during slaughter, whereas in the next pig on the line, which died more quietly, it was 6.9. The first pig would tend to follow curve 2 of fig. 1, or an even more rapid version of it, if our argument from the present results is correct, so that its pH_1 value at 45 mins. after death would be about 5.90, at a muscle temperature of 38°C. The second pig, on the other hand, would tend to follow curve 1 of fig. 1, and its pH_1 value would, therefore, be only about 6.8. According to the hypothesis that undesirably pale and watery muscle is caused by the denaturing effect on the muscle proteins of a combination of low pH and high temperature (c.f. Bendall and Lawrie 1964; Scopes, 1965), the muscle from the first pig would become pale and watery, when rigor was complete, whereas that from the second pig would have had plenty of time to cool below the danger line of about 35°C, before the pH had even fallen to 6.5, and its muscles would therefore be of normal good quality the next day.

In this connection, we may mention an interesting observation made during the measurement of extensibility changes in strips of muscle in a bath of liquid paraffin at 38°C, whether from curarised or normally slaughtered pigs. As we might expect, the conditions are right for producing pale and watery muscle,

according to our hypothesis, and this is exactly what happens, although somewhat earlier in the rigor process than might have been predicted. Thus, at about the time the muscle has lost some 25% of its ATP, and the first significant loss of extensibility has begun to occur, it also begins to turn pale, and a drop of sarcoplasmic fluid appears at its lower cut end. The pH at this time, as measured at 20°C, is about 6.3, but within the muscle itself at 38°C it would have been about 6.1 (see Bendall and Wismer-Pedersen 1962, for details of this correction). Even the lower of these values is higher than the danger line of about pH 6, which would be predicted from the detailed in vitro denaturation studies of Scopes (1965), and it is concluded that the most dangerous moment during the rigor process, at which high temperatures are likely to cause denaturation and wateriness, is when ATP, the substrate for so many of the enzymes, is first lost in significant amounts.

We might conclude from the above arguments that a combination of more or less severe struggling and excitation, during slaughter, with the long-term accelerating effect of the nervous stimuli necessary to produce the struggle, would account for most of the variability of pH_1 values in commercial practise, but it is obvious that this hypothesis will require further elaboration if it is to explain either the much more frequent occurrence of low pH_1 values in Danish Landrace than in English Large White and Landrace pigs, or the pronounced species differences, for example, the absence of any long term effect of stimulation on frog, rat or rabbit muscle (Cori 1956; Hallund and Bendall, 1965). A more elaborate hypothesis must, moreover, also be able to explain how these long-term effects are reversed in the living pig, after a period of severe excitement, whereas they are apparently irreversible in excised pieces of muscle, kept under anaerobic conditions.

We must stress that the breed and species differences, mentioned above, vanish almost entirely, when we consider the rates of post-mortem change in animals which have been immobilised before death so that no nervous stimuli can reach their muscles. Thus, from fig. 4, we see that the rates of pH fall in curarised English Large White pigs are very similar to those in myanesinised Danish Landrace, and from table 1, that the rates and time-courses of all the post-mortem changes in unstimulated, resting muscles are almost identical from species to species, except that curarised pig muscle now appears to be the slowest of all, mainly because of its very high initial pH.

The observed constancy of the rates of post mortem change in the unstimulated muscles of the various breeds and species would seem to argue against the suggestion which has often been put forward that the variability of rate, encountered in pigs in slaughterhouse practise, is due to variability in the amounts or activity of one or other of the enzymes of glycolysis (e.g. Briskey and Wismer-Pedersen 1961). This suggestion is, moreover, open to a much more serious objection, because the real rate determining step in all the post-mortem biochemical changes we have described is, in fact, the overall ATP-ase activity (Bendall 1960), and it is, therefore, here that we must first seek for variability, and not amongst the resynthesising enzymes which are subsidiary to it and triggered into activity by it.

The raison d'etre of the above argument can be simply stated:

1) the energy production of a muscle, and with it its ATP-ase activity, increases 200 to 400-fold during the contraction elicited by a stimulus, because it is the splitting of ATP by the contractile filaments of actin and myosin, which supplies this energy (Davies 1964);

2) the rate of resynthesis of ATP via the glycolytic cycle, and hence the rate of lactic acid production under anaerobic conditions, are geared to keep in step with this activity, for otherwise a muscle would quickly run out of ATP. The potential rate of lactic acid production is, therefore, also at least 200 times the resting rate, as Meyerhof originally showed in frog muscle, and Cori in rat muscle (c.f Cori 1956);

3) since the highest rates of lactic acid production, observed in the most extreme cases in resting pig muscle post-mortem, rarely if ever exceed 5 times the low and truly resting rates we have given here for curarised muscles, it follows that the glycolytic enzymes in the muscles of a living pig already have a potential rate 40 times greater than is necessary to explain these extremes.

Thus, while it may well be true that pigs of some breeds are in possession of relatively greater amounts of glycolytic enzymes than others, this has no bearing on the situation in the post-mortem muscle which already has more than enough of these enzymes to keep in step with the extremes of the resting ATP-ase activity. Or, to put it the other way round, an animal would indeed be in very poor stead, if

it had only just enough glycolytic potential to cope with the relatively feeble ATP-ase activity, observed in resting, excised muscles.

We conclude that the variability of rate of post-mortem change, encountered in pig muscle in slaughterhouse practise, is mainly attributable to the long-term effect of stimulation we have described.

It remains to elucidate the mechanism of the effect.

Summary

1) A number of Large White pigs were immobilised before death with curare, and the rate of post-mortem change in their muscles was compared with that of a group of control pigs.

2) It is shown that the effect of curare is to give very high and constant initial pH, CP and ATP values in the excised LD muscles, and a slow and constant rate of post-mortem biochemical and physical change, compared with the very variable rates observed in pigs killed by the normal method of stunning and sticking.

3) Pig muscle, curarised in this way, shows the low post-mortem rate of pH fall, characteristic of the muscles of other species, when no nervous stimuli are allowed to reach the muscles before death; for example, muscle from myanesinised rabbits, and surprisingly enough, from myanesinised Danish Landrace pigs, which otherwise often show extremely high and variable rates. Thus, there is little or no difference between breeds or species in the rate or time course of post-mortem change, when the animals are immobilised in this way before death.

4) The cause of the extreme variability of rate of pH fall, observed in pig muscle in ordinary commercial practise, must therefore be sought in the excitement and struggling, produced before and during slaughter by the methods employed, that is to say in the variable intensity of the nervous stimuli reaching the muscles.

5) It has been experimentally shown that brief electrical stimulation of the excised muscles from the curarised pigs produces not only an immediate increase in the rate of pH fall and of biochemical change, but also has a long-term accelerating effect, lasting two or more hours, so that the overall rate of change in the stimulated muscles is increased to nearly twice that of the unstimulated muscles. This long-term effect seems to be unique to pig muscle and does not occur in the muscles of rats, rabbits or frogs, which were the muscles of choice in the classical studies of the chemical changes during contraction.

6) The bearing of the stimulation effect on the variability of pH fall in commercial practise, and thus on the potential occurrence of pale and watery meat on the carcase, is discussed in detail.

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Résumé

1) Un lot de porcs Large White fut immoblisé avant le mort avec du curare, et le taux de transformation post-mortem dans les muscles fût comparé avec celui d'un groupe de contrôle.

2) Il est démontré que l'effet de curare est à donner des valeurs initiales constantes et très élevées pour le pH, le CP et le ATP dans les muscles LD excisés, ainsi que des taux de transformation post-mortem biochimique et physique lents et constants, en comparaison avec des taux variables obtenues avec des porcs tués par la méthode générale où les porcs sont abattus après avoir été assommés.

3) Le muscle de porc, ainsi curarisé, manifeste le taux ralenti de la chute de pH post-mortem qui est caractéristiques des muscles d'autres espèces quand on empêche toute stimulation nerveuse d'atteindre les muscles avant le mort; comme pour exemple dans le cas des lapins myanésinés et, ce qui est assez surprenant, dans celui des porcs Landrace danois myanésinés qui en conditions normales manifestent souvent des taux variables et très élevés. Ainsi, la différence est minime ou nulle entre les races ou les espèces, pour le taux de vitesse de la transformation post-mortem, quand les animaux sont immobilisés avant la mort par cette méthode.

4) Il faut donc rechercher la cause de la variabilité extrême du taux de chute de pH observée sur le muscle de porc de provenance commerciale dans l'excitation et la lutte suscitées, avant et durant l'abbatage, par les méthodes employées, c'est à dire dans l'intensité variable des stimulation nerveuses qui atteignent les muscles.

5) Il a été démontré expérimentalement qu'une courte stimulation électrique des muscles excisés des porcs traités a curare, produit non seulement une augmentation immédiate de la vitesse de la chute du pH et de la transformation biochimique, mais aussi une accélération à long terme, durant 2 heures ou plus, si bien que le taux de transformation global dans les muscles stimulés devient deux fois celui des muscles non stimulés. Cet effet à long terme semble s'appliquer uniquement au muscle de porc et ne se manifeste ni dans les muscles de lapin ni dans ceux de rat ni de grenouille, qui formaient pour les études classiques sur les transformations chimiques au cours de la contraction, les muscles prédominants.

6) Le rapport entre l'effet de la stimulation et la variabilité de la vitesse de chute du pH qu'on trouve dans la practique commerciale, et par là le rapport entre cet effet et la possibilité d'une viande pâle et exsudative sur la carcasse sont détaillés dans nos discussions.

Zusammenfassung

1) Mehrere Large-White-Schweine wurden vor dem Tode durch Kurare gelähmt, und die Geschwindigkeit der postmortalen Veränderung seiner Muskeln wurde mit der einer Anzahl Kontrollschweine verglichen.

2) Festgestellt wurde, dass Kurare durch die Hervorbringung sehr hoher und konstanter Anfange-pH-, CP- und ATP-Werte in den ausgeschnittenen LD Muskeln, und einer langsamen und konstanten Geschwindigkeit der postmortalen biochemischen und physikalischen Veränderung wirkt, im Vergleich mit den sehr variablen Geschwindigkeiten, die in den nach üblichem Verfahren durch Betäubung und Stechung geschlachtenen Schweinen zu beobachten waren.

3) Der Schweinemuskel, auf diese Weise kurariert, zeigt die niedrige postmortale Geschwindigkeit des pH-Abfalls, die die Muskeln anderer Arten charakterisiert, wenn man den Muskeln vor dem Tode keine Nervenreize zukommen lässt; zum Beispiel, Muskeln von myanesinisierten Kaninchen und, merkwürdigerweise, von myanesinisierten dänischen Landrasse-Schweinen, die sonst häufig übermässig hohe und variable Geschwindigkeiten zeigen. Es gibt also wenig oder keinen Unterschied zwischen Zuchten oder Sorten in der Geschwindigkeit oder im Zeitlauf der postmortalen Veränderungen, wenn die Tiere vor dem Tode auf diese Weise gelähmt sind.

4) Man soll daher die Ursache der im Schweinemuskel in der gewöhblichen Handelspraxis beobachteten übermässigen Variabilität der Geschwindigkeit des pH-Wert-Abfalls in der Aufregung und Anstrengung suchen, die das verwendete Verfahren vor dem Schlachten und während des Schlachtens zur Folge hat, das heisst in der variablen Stärke der Nervenreize, die die Muskeln erreichen.

5) Es wurde durch Experiment festgestellt, dass kurze elektrische Reizung der von den kurarierten Schweinen ausgeschnitten Muskeln nicht nur ein sofortiges Zunehmen der Geschwindigkeit des pH-Wert-Abfalls und der biochemischen Veränderung hervorbringt, sondern auch eine dauernde Beschleunigungswirkung hat, die zwei oder mehr Stunden dauert, so dass die Gesamtgeschwindigkeit der Veränderung in den gereizten Muskeln bis um fast das Doppelte jener der ungereizten Muskeln erhöht wird. Diese dauernde Wirkung scheint dem Schweinemuskel eigenschäftlich zu sein und kommt in den Muskeln von Ratten, Kaninchen oder Frösche nicht vor, die in den berühmten Studien der chemischen Veränderungen während der Zusammenziehung die gewählten Muskeln waren.

6) Der Zusammenhang der Reizungswirkung mit der Variabilität des pH-Wert-Abfalls in der Handelspraxis, und daher mit dem möglichen Vorkommen des blassen und wässrigen Fleisches auf dem Tierkörper, wird ausführlich diskutiert.

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Table 1

Time course of post-mortem biochemical and physical changes in LD muscles of various species of animal.

Species and treatment.	pH Initial	pH Ultimate	Rate of pH fall per hr. (pH 7 to 6)	Time in mins. for ½ change of ATP	Time in mins. for ½ change of Extensibility
Pig - LW. Curare	7.30	5.40	0.21	300 (220)[x]	290 (210)[x]
÷ stim[n]	7.20	5.40	0.36	160 (117)[x]	- -
DL. Myanesin	7.00	5.50	0.24	200	220
+ stim[n]	6.90	5.40	0.42	-	-
Rabbit - Myanesin	7.10	5.70	0.27	180 (160)[x]	200 (180)[x]
+ stim[n]	7.00	5.70	0.27	180	200
Beef - Untreated	7.00	5.40	0.27	220	260

[x]times in brackets corrected to initial pH 7.00

Danish Landrace values (DL) from Hallund and Bendall (unpublished)
English Large White values (LW) from present results.
Rabbit values from Bendall and Lawrie (1962) and Hallund and Bendall.
Beef values from Marsh (1954).

Fig. 1. pH/time curves of L.D. muscles from curarised pigs, and normally slaughtered pigs.

Curve 1. Unstimulated 'curarised' muscles (6 animals)
2. Stimulated " " (4 ")
3. Unstimulated normal " (4 ")

Standard errors of pH measurements shown at each time point, as vertical bars (N = 6 in each case)

Average curve of loss of extensibility shown for 6 animals of group 1. Temp. 35°C.

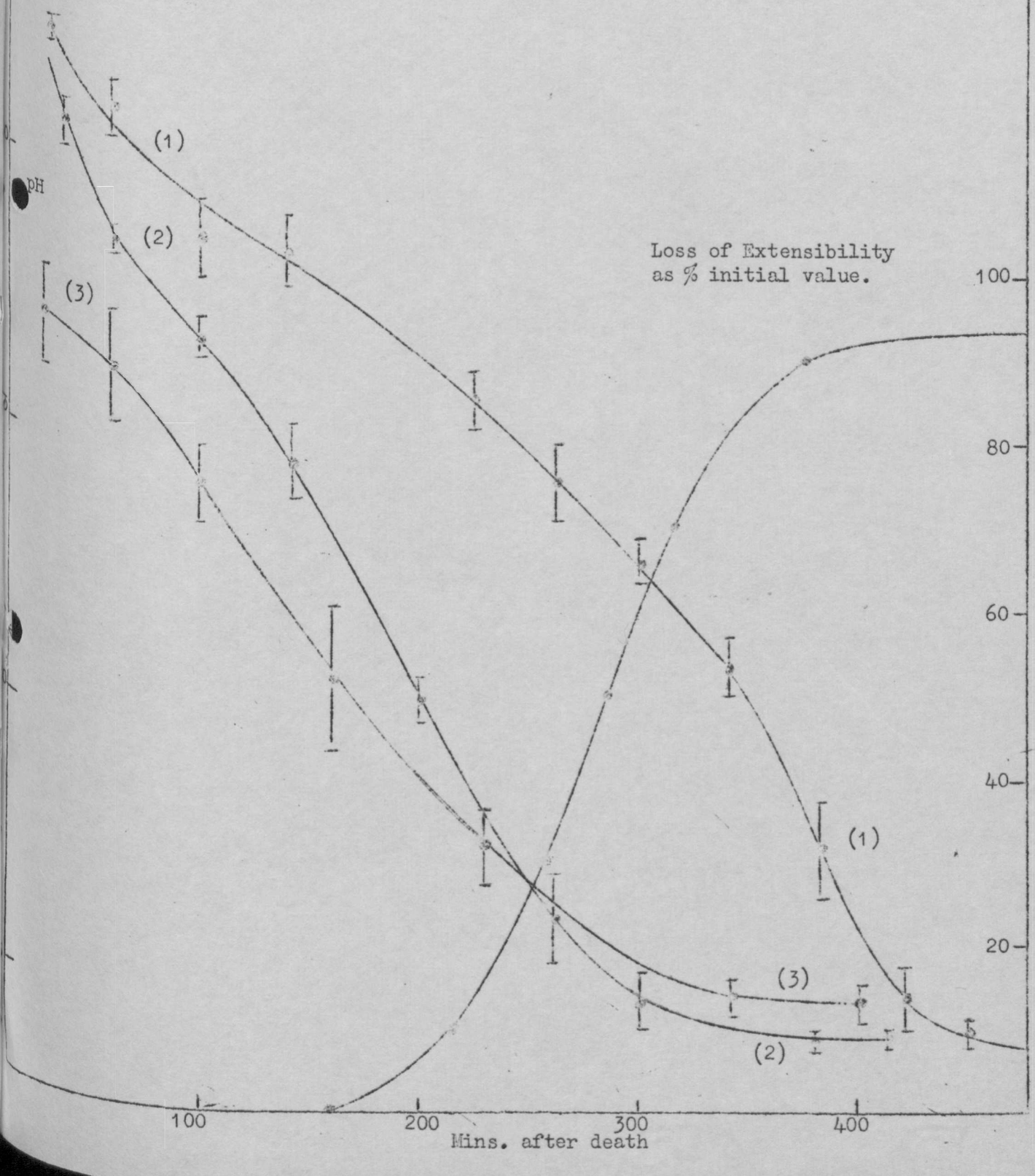


Fig. 2. The variability of rates of pH fall and extensibility changes in the LD muscles of Large White pigs, stunned and stuck in the normal way. Fig. 2a shows the pH changes at either end of a strip taken from pig 2 of the control group, and fig. 2b the same for pig 3. Extensibility changes were measured on a separate strip in each case. Temperature 38°C.

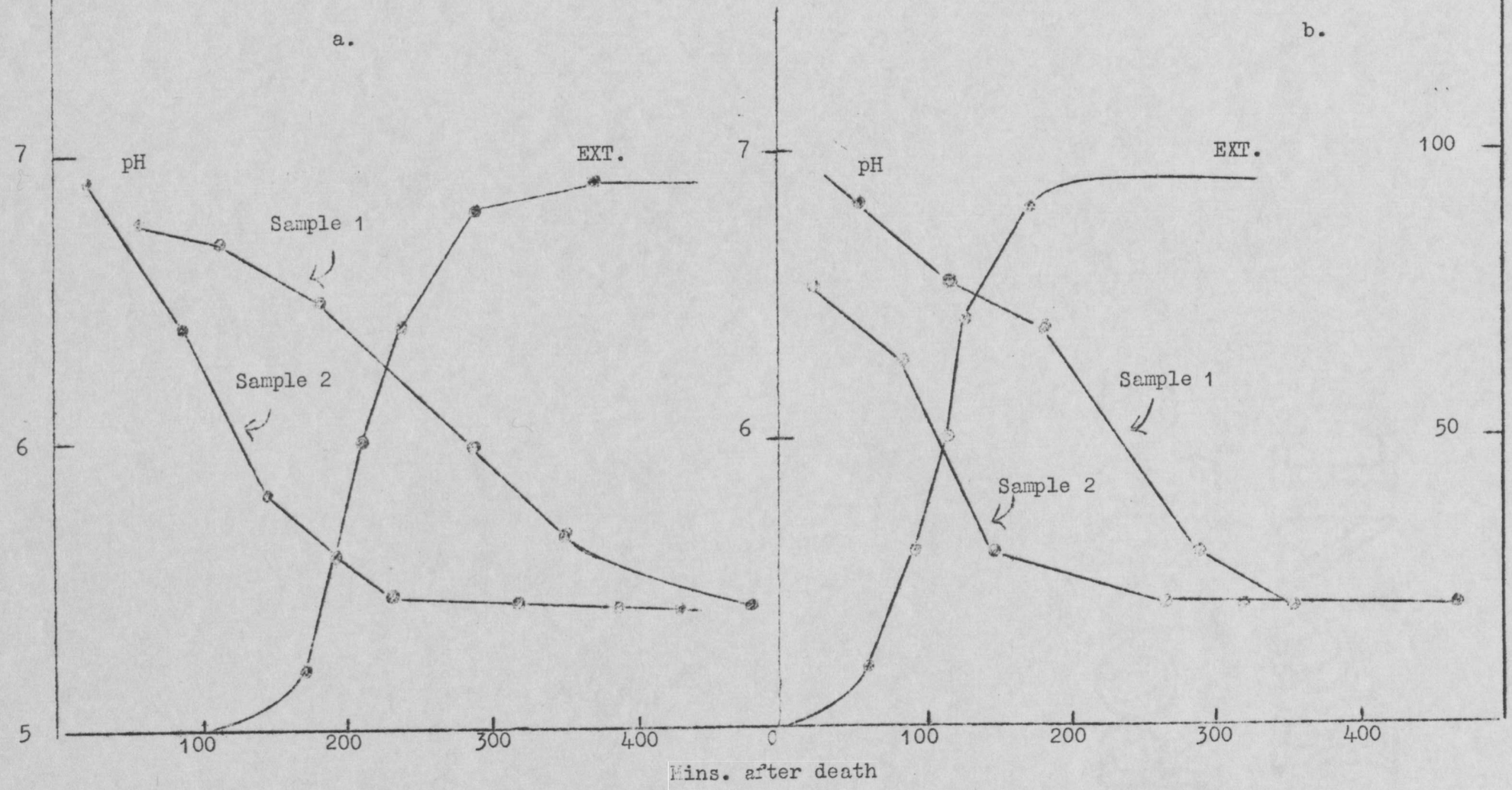
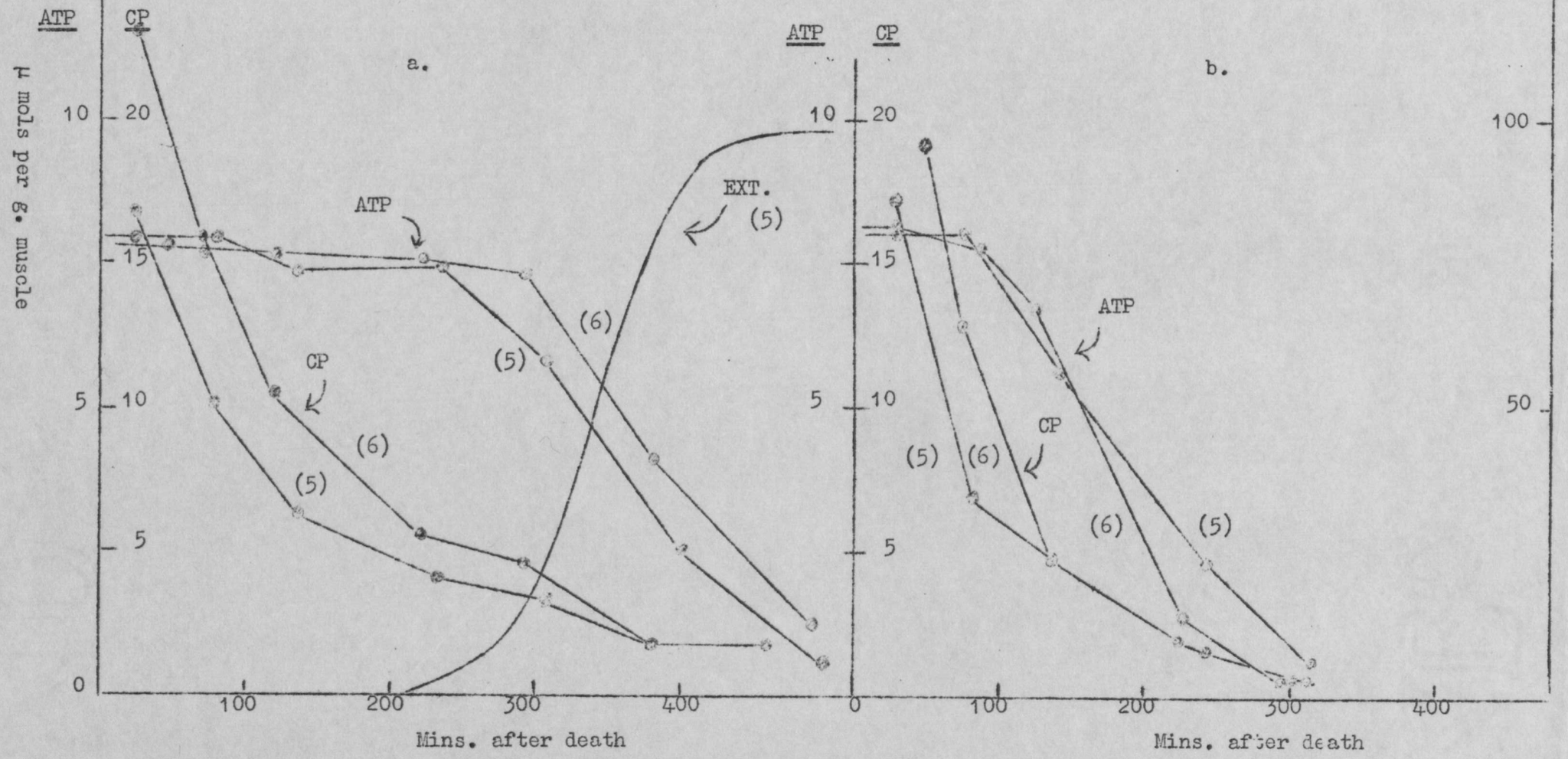


Fig. 3. Time course of changes in creatine phosphate (CP) and ATP in stimulated and unstimulated muscle samples from two curarised pigs (pigs 5 & 6). The extensibility change in one unstimulated sample (pig. 5) is also shown.

Fig. 3a -- unstimulated samples.
Fig. 3b -- stimulated " .

Temperature 38°C.



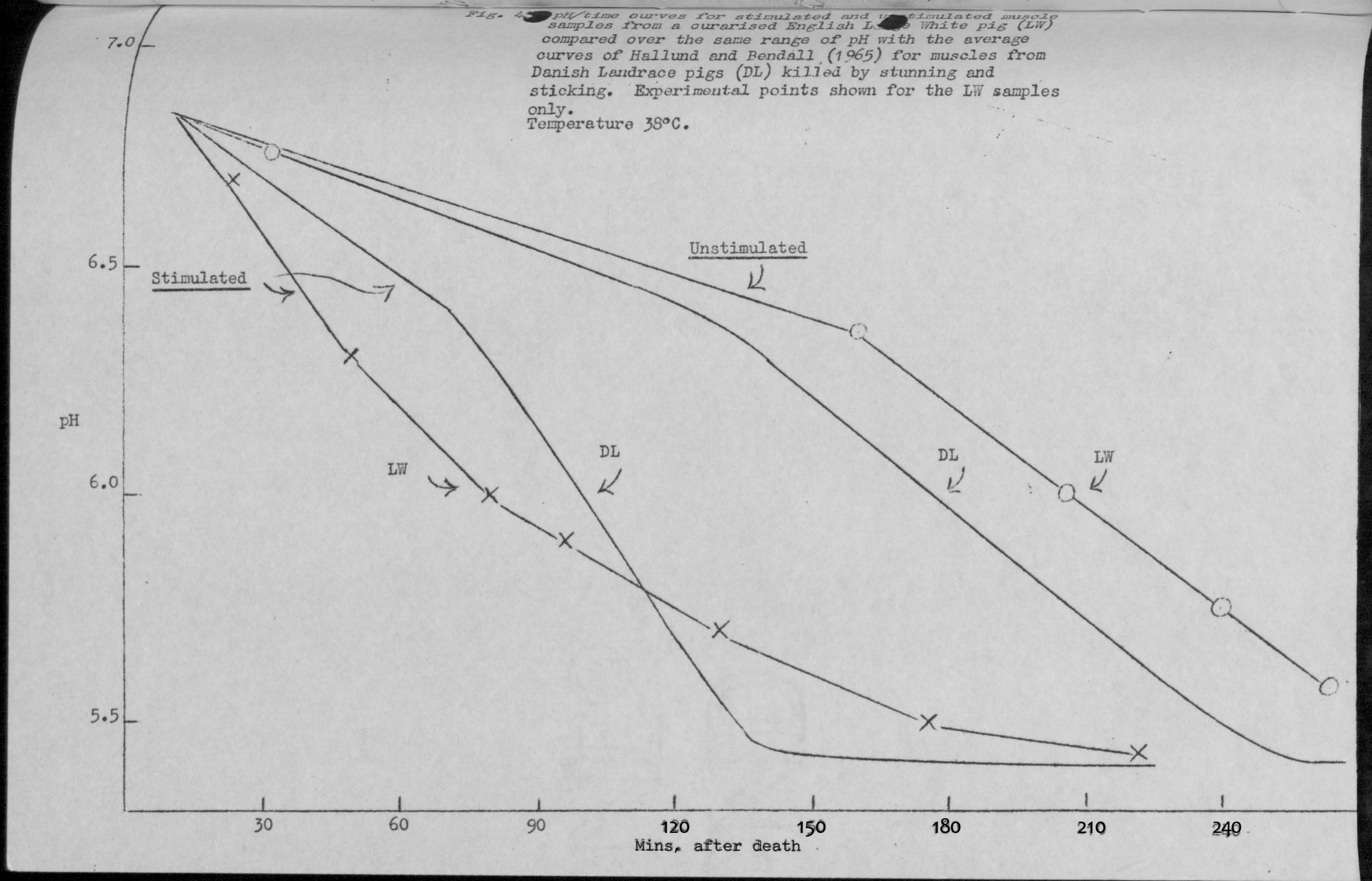


Fig. 4 pH/time curves for stimulated and unstimulated muscle samples from a curarised English Large White pig (LW) compared over the same range of pH with the average curves of Hallund and Bendall (1965) for muscles from Danish Landrace pigs (DL) killed by stunning and sticking. Experimental points shown for the LW samples only.
Temperature 38°C.

Fig. 5. Time course of pH and extensibility changes in muscle samples from two Danish Landrace pigs, immobilised for 5 mins. before death with myanesin, compared with the average curves for the six curarised English Large White pigs over the same range of pH.
Temperature 38°C.

Broken lines and circles --- Danish Landrace

Full lines --- English Large White.