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Symposium I

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Mechanisms controlling glycolysis II

Physiological considerations

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It is clear from the previous paper (Scopes, 1971) that the mechanisms of most interest in the present context are those concerned with the rate and extent of post-mortem glycolysis in muscle. At the present time it is not possible to pinpoint exactly the physiological mechanism which determines the pH at which glycolysis ceases in a muscle adequately endowed with glycogen at the moment of death, and the suggestion offered by Scopes (1971) must suffice. However, it is generally held that an association does exist between the rate and extent of post mortem change in muscle i.e. rapid rates of pH fall are often accompanied by unusually low ultimate pH, and the two may share a common physiology.

The importance of myofibrillar ATPase activity as a controlling mechanism of glycolysis can now be demonstrated by physiological experiment as well as in the biochemical terms previously described. It is, perhaps, worth reiterating the nature of the physiological processes, for it is from these that we can most easily draw information of practical value to the meat industry. In doing so I shall consider the metabolism of pig muscle. Pig muscle is, perhaps, of greatest interest because the normal course of post mortem glycolysis in the economically important muscles of the pig is such that increases in glycolytic rate often lead to excessive denaturation of the soluble sarcoplasmic (and even of the myofibrillar) proteins. This causes loss of their ability to bind water and their precipitation on to the structural proteins of muscle, and gives rise to the well known P.S.E. condition in meat.

Although the same physiological and biochemical principles also apply to both cattle and sheep, the P.S.E. condition is not commonly found in these species. This is primarily because the time scale of muscle glycolysis is sufficiently extended for carcass temperatures to be reduced by conventional refrigeration practices to a point where the interaction between temperature and acid pH (in this context less than $\sim$6.0) will not cause excessive denaturation of muscle proteins.

It is first of all necessary to demonstrate that changes in the rate of ATP turnover in living muscle can be reflected in the metabolism of that muscle post mortem. Bendall (1966) convincingly demonstrated this effect in a group of Large White pigs which were anaesthetised and curarised at the time they were stuck. This technique markedly reduces the extent to which nervous stimuli pass across the motor end-plates into muscle fibres thus preventing stimulation of muscle activity. The rate of glycolysis was markedly retarded in the muscles of the treated animals, compared with those of conventionally slaughtered pigs. On the other hand, direct stimulation of the curarised muscle, which is possible when electrical impulses are applied directly to the muscle, led to a large increase in the previously much retarded rate of glycolysis. Bendall concluded that it is probably the eliciting of the neuro muscular response which is most commonly responsible for the production of inferior quality pork. One may also extend this observation to cover the effects of continued neuro-muscular stimulation such as an animal might encounter, for example, during transportation in unfavourable conditions, or the common lairageing of groups of animals from different sources. In this case, the continuing neuro muscular stimulation will lead ultimately to glycogen depletion in the living muscle and to the production of meat of a dark cutting, high pH, type post mortem.

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Apparent exceptions to this general case do occur, however, and unfortunately these exceptions present themselves in those breeds of pig whose meat quality is generally poor, e.g. Pietrain or Poland China. It has been shown (see Lister 1970), that curarisation is only partially effective in reducing the post mortem rate of pH fall in these breeds, where it is not uncommon to observe the completion of glycolysis at pH values below 5.5, within 10-15 minutes of slaughter.

A more effective relaxation of muscle can be achieved in the Pietrain and Poland China breeds by the intravenous administration of fatal or near fatal doses of magnesium sulphate. It is not known, however, how magnesium sulphate solution achieves this effect, for it has properties which relate to the central nervous system as well as to neuro muscular physiology and the inhibition of ATPase activity in particular, but whatever mechanism is responsible, the profound relaxation of the musculature of animals so treated is clearly apparent.

This latter experiment, more than any other, in my opinion, demonstrates the overwhelming importance of muscle stimulation in the context of the P.S.E. meat syndrome, whether the animals are similar to the Large White or Pietrain types. In the experiments outlined above, treated and untreated pigs of a breed group were from common stock and their physiological constitutions might be expected to be closely similar. Yet, by achieving a profound muscular relaxation at the time of death, it was possible to overcome all the purported inadequacies of enzyme or hormone levels, which presumably were present in the treated animals just as they were in the untreated animals whose muscles responded to slaughter in the usual fashion, and retard glycolysis to produce meat of acceptable quality (Lister and Ratcliffe, 1970).

The problem to be solved, therefore, is not whether a given rate of glycolysis can be supported by the usual biochemical pathways in muscle of a particular type (Scopes (1971) concluded that the potential rates of glycolysis in muscle always greatly exceed the observed rate) but how such a rate is triggered. It is the search for the trigger mechanism, especially in those breeds which suffer a hypersensitive response, which is of most concern in the physiological context.

Various suggestions have been offered to explain the nature of the untoward metabolic response in some animals, and most can ultimately be explained in terms of the increased utilisation of ATP, triggered by an unknown mechanism. For instance, it has for long been considered that the extent of anoxia suffered by an animal at slaughter was of key importance. Accordingly experiments were conducted (Lister et al 1970) on the so-called stress susceptible and resistant varieties of pig (Poland China or Chester White) to examine the effect of administering oxygen or nitrogen at high concentrations to anaesthetised animals, prior to their exsanguination. It was found that animals with a normally slow resting turnover of ATP were not affected by either treatment in terms of their muscle metabolism post mortem, whilst the administration of pure oxygen to the stress susceptible pigs had no appreciable effect post mortem either, for the rate of muscle metabolism was sufficiently high for any beneficial effects there might have been to be nullified by the effects of the anoxia produced by sticking and evisceration.

It is clear, therefore, that the anoxia associated with the slaughter process will not itself be in any way damaging to muscle metabolism post mortem if the muscle is not metabolically stimulated at the time of death. If it is, high tensions of oxygen in the blood will be only of temporary advantage. One must also conclude that small differencies which may be found from breed to breed in the inherent capability of particular muscles for aerobic or anaerobic metabolism, i.e. whether it contains more or fewer red or white fibres, will not

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materially alter this conclusion so far as the response to anoxia at slaughter is concerned. This is not to deny, of course, that muscles which can be clearly categorised as red or white types (see Beatty & Bocek, 1970) show different patterns of glycolysis post mortem both in terms of rate and extent; the red type showing a slower, less extensive change than the white. In view of these latter characteristics, examination of the physiology and biochemistry of these fibre types, and the ways in which each type is triggered into activity, may well be of importance in the present context.

The concept of stress susceptibility in animals inevitably gave rise to investigations of various aspects of endocrine function and there would seem to be other reasons to support the idea that differences may exist in the endocrine function of animals with different bodily proportions or types e.g. large or small, fat or lean (see Lister, 1970). Judge and his co workers (Judge, 1971) have shown that although the production of ACTH by the pituitary is increased in animals of a stress susceptible type, the production of adrenal corticoids is not. Our own studies would support the conclusion that the adrenals of pigs of such a type are relatively unresponsive to direct stimulation (Lister, 1971).

Even though some aspects of endocrine performance can be shown to be different from one type of animal to another, it is by no means clear how these characteristics are involved in the various patterns of glycolysis to be found. The evidence previously cited concerning the effects of curare in Pietrain and Large White pigs suggested that the hypersensitive response in Pietrain muscle is, perhaps, initiated in the muscle fibre itself, due to an electrolyte imbalance at the cell membranes. In view of its central role in maintaining tissue electrolyte balance, it is not unreasonable to implicate the adrenal gland in the condition and, indeed, it is possible to show by appropriate therapy that alleviation of a potential adrenal insufficiency can retard the progress of post mortem glycolysis even in the muscle of Pietrain pigs (Lister 1971).

We must, however, still conclude that the site of the hypersensitive response which triggers an unusually rapid glycolysis in certain muscles of some types of animal and pigs in particular, still eludes us. It is, however, difficult to imagine that this state of affairs can continue indefinitely in the light of the enormous advances currently being made in the fields of biochemistry and physiology generally.

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